A REVISION OF SAHNI'S TYPES OF THE BRACHIOPOD SUBFAMILY CARNEITHYRIDINAE

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CONTENTS

SYNOPSIS

Sahni's type material of Upper Campanian and Lower Maastrichtian carneithyridine brachio-pods is reviewed and the type specimens refigured. The present material of carneithyridines in English collections is discussed. It is concluded that only one genus, *Carneithyris*, is present and is represented by two species, *Carneithyris carnea* from the Upper Campanian and *Carneithyris subcardinalis* from the Lower Maastrichtian. The stratigraphical variation of the genus, its palaeoecology and relationship to different facies are examined.

I. INTRODUCTION

THE Upper Campanian and Lower Maastrichtian terebratulids, formerly known under the names *Terebratula carnea* J. Sowerby (1812) and *T. elongata* J. de C. Sowerby (1823), were split up by Sahni (1925, 1925a, 1929) into seven genera represented by 22 species. In the course of work on Maastrichtian and Danian carneithyridine terebratulid material from Denmark (Asgaard 1963) I found it necessary to study the types of Sahni, and this led to many visits to the English museums housing the types and to fieldwork in the Norwich area in the years 1962 to 1972. This paper is a result of these investigations. A review of the types is followed by a discussion of the validity of the genera and species. It was found that Sahni's types have suffered much wear since they were figured.

The possibility that seven closely related genera represented by 22 species could have existed in the same area within the relatively short time-span covering the Upper Campanian and Lower Maastrichtian cannot be excluded. However, it can be shown that the premises on which these genera and species were founded are not tenable and that the phylogenetic tree created by Sahni (1925a) does not have a firm stratigraphical footing.

The conclusion of this paper is that the English material represents only one genus with two species, viz. *Carneithyris carnea* (J. Sowerby 1812) from the Upper Campanian and *Carneithyris subcardinalis* (Sahni 1925) from the Maastrichtian. The geographical and stratigraphical variation of these species is described. An attempt was made to demonstrate the variation statistically but this was not found to be possible with the present material.

The representatives of *Carneithyris* treated here are chiefly from the white chalk facies of Campanian and Maastrichtian age. However, the discussion is supple-mented by reference to forms from other facies of the Upper Cretaceous and Lower Tertiary where these can shed light on the variation and phylogeny of the genus.

III. HISTORICAL REVIEW

Terebratula carnea J. Sowerby 1812 and *Terebratula elongata* J. de C. Sowerby 1823 are among the species of terebratulids most quoted in the literature on the Upper Cretaceous White Chalk of northern Europe.   Davidson (1854 : 67) placed *T. elongata* in synonymy with *T. carnea* and figured several specimens from the Upper Campanian of Norfolk.

The English Campanian–Maastrichtian terebratulids were treated comprehensively by Sahni (1925, 1925a, 1929, 1958).   In 1925 he based his work on material in the Institute of Geological Sciences, London, and the Castle Museum, Norwich. Since he had seen the collections of neither Sowerby nor Davidson in the British Museum (Natural History), London, he found it impossible to identify any of the specimens available to him with the true *T. carnea* and *T. elongata*.   Nevertheless, he erected four new genera to cover what different authors until then had called *T. carnea* and *T. elongata*, viz. *Pulchrithyris*, *Carneithyris*, *Chatwinothyris* and *Ellipsothyris*.   In the same paper Sahni (1925) erected the following 13 species :

Pulchrithyris gracilis	*Magnithyris magna*
P. extensa	*Chatwinothyris subcardinalis*
Carneithyris subpentagonalis	*Ch. symphytica*
C. circularis	*Piarothyris rotunda*
C. variabilis	*Ellipsothyris similis*
C. acuminata	*Ornithothyris carinata*
C. norvicensis	

Shortly after this he (1925a) added the following five new species to the list :

Carneithyris daviesi	*Chatwinothyris curiosa*
C. subovalis	*Ch. gibbosa*
C. uniplicata	

and, concerning the evolution and ontogeny of the species of *Carneithyris*, he arrived at the following conclusions (1925a : 502) :

1.   That the type of hinge-parts and cardinal process is of considerable importance in the study of Chalk Terebratulids.
2.   That the cardinal process shows a distinct line of evolution in the genus *Carneithyris* expressed by :
(a)   Change in shape from pyramidal to globular.
(b)   Greater and greater development of its apophyses.
(c)   Change in position with respect to the surrounding hinge-parts.
3.   That these changes are repeated in phylogeny as well as in ontogeny.

Sahni (1925a : pl. 25) arranged the following table to illustrate the changes in ontogeny and phylogeny :

		ontogeny	*phylogeny*
Stage IV	*Carneithyris subpentagonalis* (fig. 1)		
	C. subpentagonalis (fig. 7)		*C. variabilis* (fig. 2)
Stage III	*C. subpentagonalis* (fig. 8)		*C. daviesi* (fig. 3)
Stage II	*C. subpentagonalis* (figs 9, 10)		*C. subovalis* (fig. 4)
			C. subovalis (fig. 5)
Stage I	*C. subpentagonalis* (fig. 11)		*C. uniplicata* (fig. 6)

From this it must naturally follow that *C. uniplicata* is found in strata considerably older than those bearing *C. subpentagonalis* and *C. variabilis*.

In 1929 the species erected formally and correctly in 1925a Sahni again described as new and, in addition, the new species *Carneithyris ornata* and *Magnithyris truncata* were erected. In the same year he redescribed and refigured *Carneithyris carnea* and *C. elongata* for the first time.

In 1958 Sahni published a description of the Campanian and Maastrichtian terebratulids belonging to the *Carneithyris* group from A. W. Rowe's collection which, in about 1926, had come into the possession of the British Museum (Natural History). No new species were described, but more than 50 specimens of *Chatwinothyris subcardinalis* were examined and 17 specimens of *Carneithyris gracilis* and two of *C. carnea* from the Campanian of the Norwich area were also dealt with. Thus, by 1958, 19 species of carneithyridines from the Upper Campanian and three species from the Lower Maastrichtian of the Norwich area were known.

From the Maastrichtian Craie Phosphaté de Ciply, Belgium, Sahni (1929 : 41–2) erected the new species *Chatwinothyris ciplyensis* and placed some Danian specimens known under the name '*Terebratula lens*' Nilsson in *Chatwinothyris*.

Between 1925 and 1958 *Carneithyris* and *Chatwinothyris* were reported from the Campanian, Maastrichtian and Danian of Sweden (Hägg 1940, 1954), Denmark (Rosenkrantz 1945), Poland (Kongiel 1935) and Bulgaria (Tzankov 1940 ; Zakharieva-Kovaceva 1947). In 1965 Steinich monographed the Upper Lower Maastrichtian brachiopods from the island of Rügen, Germany, and gave an extremely comprehensive description of *Chatwinothyris subcardinalis*, including a first description of its ontogeny and variation.

Muir-Wood (1965 : 799) erected a new subfamily of terebratulids, the Carneithyridinae, represented only by the two genera *Carneithyris* and *Chatwinothyris*. Concerning *Pulchrithyris*, *Ellipsothyris*, *Magnithyris*, *Ornithothyris* and *Piarothyris* she wrote : 'These genera are considered to be variants of *Carneithyris* and not distinct genera.'

The Upper Cretaceous terebratulids of the Middle Vistula valley, Poland, were described by Popiel-Barczyk (1968). Among these were the carneithyridines *Carneithyris subpentagonalis*, *C. carnea* and *C. circularis* from the Campanian and Maastrichtian ; *C. elongata* from the Upper Maastrichtian ; and, in addition, *Chatwinothyris subcardinalis*, *Ch. curiosa* and *Ch. lens* from the Upper Maastrichtian. In her identification of the species she considered that external features were more

dependable than internal ones, and (1968 : 23, 30) that the cardinalia in each species varied considerably, depending on the age of the individual specimen.

Asgaard (1970) discussed Sahni's specimens of *Chatwinothyris lens* and showed that they were not the true Upper Danian *Terebratula lens* of Nilsson (1827) but the slightly older *Terebratula incisa* Buch (1835) ; she considered furthermore that *Chatwinothyris* was a synonym of *Carneithyris*.

Surlyk (1972 : 24) also considered *Chatwinothyris* to be congeneric with *Carneithyris* and described the special adaptation of the Maastrichtian white chalk *C. subcardinalis* to a free-living mode of life as a 'self-righting tumbler'.

IV. THE PROVENANCE OF THE TYPE MATERIAL

During the period 1925–27, when Sahni wrote his first three papers, practically every carneithyridine in the collections of the British Museum (Natural History), the Geological Survey of Great Britain, now the Institute of Geological Sciences, London, and the Norwich Castle Museum was opened and dissected, and designated as a type, figured or identified.   Later the British Museum (Natural History) came into the possession of A. W. Rowe's stratigraphically well-documented collection of brachiopods, part of which formed the basis of Sahni's latest paper (1958) on the British terebratulids, but these specimens were not dissected.

The classical 'Upper Chalk of Norwich, Zone of *Belemnitella mucronata*' was long considered a single stratigraphical unit and collectors and museum curators often considered it unimportant to state on the labels from which pits the specimens originated.   However, the careful stratigraphical collections made by Rowe and Brydone showed that the Upper Chalk of Norwich could be split up into Campanian and Lower Maastrichtian parts (Brydone 1908, 1909, 1938).   Mainly on the basis of Brydone's work Peake & Hancock (1961 : 297, fig. 3) divided the classical Norwich Chalk into six subdivisions :

	estimated thickness
Paramoudra Chalk	23 m
Beeston Chalk	23 m
Catton Sponge Bed (a complex of incipient hardgrounds at the top of :)	
Weybourne Chalk	23 m
Eaton Chalk	15 m
Basal *mucronata* Chalk	15 m

Thus the Upper Campanian (zone of *Belemnitella mucronata* s.l.) is about 100 m thick.   Above this follows a Lower Maastrichtian series estimated to be about 33·5 m thick, which is only known well from glacially transported masses.   The Campanian/Maastrichtian contact has not yet been observed with certainty in the Norfolk area (see p. 360).   The subdivisions of Peake & Hancock (1961) will be used in this paper.

The specimens in Sahni's material which have labels with a locality name other than 'Upper Chalk, Norwich' originate from the following localities :

'*Trowse.*' According to the Sowerbys (1812, 1823) the types of *Terebratula carnea* and *T. elongata* came from this locality. Several pits in the Trowse area in high Beeston Chalk may have contributed towards what was called 'Trowse' on early 19th-century museum labels. Later on this designation might also have included *Whitlingham* (Crown Point Pit), which was opened in the late 19th century, exposing high Paramoudra Chalk.

'*Thorpe.*' Several types are labelled 'Thorpe'. This locality name also covers a number of pits which were found in the area stretching eastwards from near the centre of Norwich to Postwick. *Lollard's Pit* was in high Beeston Chalk ; it was the source of *Mosasaurus* remains and therefore might include some part of the hardground complex which is considered to separate the Beeston Chalk from the Paramoudra Chalk (Peake & Hancock 1970). The pit called *St James's Hollow* was in strata of approximately the same age. Two large pits known as *Thorpe Hamlets* were intensively worked in the early 19th century and much material collected by Fitch, King, S. Woodward and others may have come from here. These pits were also in high Beeston Chalk. Further east of these was the locality known as *Thorpe Limekiln* or *Thorpe Lunatic Asylum Pit*. The chalk in it was quite markedly yellow and a section about 2 m high could still be seen when I visited it in 1962. The pit is considered to have been in high Paramoudra Chalk. It was available to the early collectors, and later yielded much material to Rowe. The pit at *Thorpe Tollgate* also contained yellow chalk from high Paramoudra Chalk and was worked in the early 19th century. Further east was the *Postwick Grove* pit which exposed chalk of the same age as Thorpe Tollgate. These two pits exposed possibly the highest *in situ* Paramoudra Chalk in Norfolk.

Mousehold, earlier called *Magdalen Chapel*. From this pit Rowe collected many large carneithyridines and according to E. F. Owen, N. B. Peake and C. J. Wood (personal communications 1972) this was the pit which yielded most of Bayfield's collection of extremely large, often gerontic specimens. Now in the British Museum (Natural History), this formed an important part of Sahni's material ; it contains eight of his types, two possible types (one of which is figured), one figured specimen and three identified to species. The pit is considered to have been in Beeston Chalk and probably high in the lower half of it.

· '*Catton.*' Some of Sahni's material originated from 'Catton by Norwich' (collected by H. M. Muir-Wood) and '? Norwich' (collected by Sahni). According to E. F. Owen (personal communication 1971) Sahni and Muir-Wood visited the Norwich area on one occasion guided by the late T. H. Withers, and collected in *Attoe's Pit*, Catton. At that time this pit exposed Weybourne Chalk at the bottom, with the Catton Sponge Bed complex at its summit, overlain by a considerable section in low Beeston Chalk.

Trimingham. These outcrops of glacially transported masses along the coast between Sidestrand and Mundesley have yielded much material to the old collections. The masses were mapped and described in detail by Brydone (1908). Brydone

(1938 : 7) concluded that the lower part of the Trimingham Chalk was of approximately the same age as the White Chalk of Rügen, Germany, and the upper part equivalent to the Tuffeau of Maastricht, Holland. The following subdivision by Brydone of the Trimingham Chalk has also been used by Peake & Hancock (1961, 1970) and Wood (1967) :

	estimated thickness	belemnite zones (Wood 1967)
Grey Beds	c. 6·7 m	base of *Belemnella occidentalis cimbrica* Zone
White Chalk with '*Ostrea lunata*'	c. 6·1 m	*B. occidentalis occidentalis* Zone
White Chalk without '*O. lunata*'	c. 2·7 m	
Sponge Beds	c. 3·7 m	restricted *B. lanceolata* Zone
Porosphaera Beds	c. 4·3 m	

According to Peake & Hancock (1961 : 323) the White Chalk with and without '*Ostrea lunata*' yielded most of the old material labelled 'Trimingham'. F. Surlyk (personal communication 1973) considers the Grey Chalk to belong to his Zone 5 on the basis of the brachiopods (Surlyk 1970) while the lower part of the Sponge Beds and the *Porosphaera* Beds predate brachiopod zones known from the Lower Maastrichtian of Denmark.

The old collection of Norwich Castle Museum. This collection was the basis for parts of Sahni's first paper (1925) and it contains ten types and two figured specimens of carneithyridines. It contains specimens from the Fitch, King and S. Woodward collections, but owing to inadequate curation at the beginning of this century the original labels were separated from the specimens. Apart from figured specimens and those marked with ink, it is impossible even to ascertain from which of the classical collections the brachiopods came and their exact localities are unknown (B. McWilliams, personal communication 1972).

For much of this section I am greatly indebted to Mr C. J. Wood, who has generously put at my disposal his extensive knowledge on the stratigraphical position of pits in the Norwich area, many of which are now obliterated.

V. REVIEW OF SAHNI'S MATERIAL OF CARNEITHYRIDINES

In this and the following sections the glossary of morphological terms used in the *Treatise on Invertebrate Paleontology*, **H** (1965) will be followed. Specimens treated in this chapter are housed in the British Museum (Natural History) (numbers with B), the Institute of Geological Sciences (GSM) and the Norwich Castle Museum old collections (CMN or KCN). A name in parentheses after the number of the specimen is that of the collector ; following this is the locality as originally given. In the plates no attempt has been made to retouch the photographs : the figures have been largely arranged according to the development of the cardinalia.

Carneithyris carnea (J. Sowerby, 1812)

Pl. 1, figs 1–3 ; Pl. 3, fig. 3 ; Pl. 5, fig. 9 ; Text-fig. 2B

Lectotype (sel. Sahni, 1929) : B 49836 (Sowerby) 'Trowse' (Pl. 1, fig. 1)
 Sowerby, 1812 : 47 ; pl. 15, fig. 5
 Sahni, 1929 : 31–2 ; pl. 4, fig. 34
 The lectotype is here refigured.

Paralectotype ('Syntype' of Sahni) : B 49837 (Sowerby) 'Trowse' (Pl. 1, fig. 2)
 Sowerby, 1812 : 47 ; pl. 15, fig. 6
 Sahni, 1929 : pl. 9, fig. 26
 The brachial valve of the 'syntype', last figured by Sahni, has since been lost and
only the pedicle valve remains.

'Plesiotype'[1] of Sahni : B 45600 (Bayfield) 'Norwich' (Pl. 3, fig. 3)
 Sahni, 1929 : pl. 9, fig. 25
 This is practically identical in cardinalia and external features with the paratype
B 45603 of *C. circularis* (Pl. 3, fig. 2), also from the Bayfield collection. It is also
very similar to the holotypes of *C. subovalis*, *C. uniplicata* and *Ellipsothyris similis*
(Pl. 4, figs 3, 9, 10).

Others : B 51289 (Rowe) 'Whitlingham'
 Sahni, 1958 : 17 ; pl. 6, figs 8a–c
 Of the three specimens from Rowe's collection, only this one has been returned
to it.

 B 51274 and B 51288 (Rowe), said to be from Norwich
 Sahni, 1958 : pl. 6, figs 9a–c, 10a–b
 These have not been found in the collection : the specimen now numbered
B 51274 is clearly not that which Sahni figured under that number (see p. 330).

 ? B 49852 (Davidson) 'Trimingham' (Pl. 1, fig. 3)
 Davidson, 1854 : pl. 8, fig. 1
 This specimen was not mentioned by Sahni. Although it is said to be from
Trimingham, its pink colour shows it to be Campanian.

 26 KCN and 27 KCN 'Upper Chalk, Norwich' (Pl. 5, fig. 9 ; Text-fig. 2B)
 Sahni, 1929 : pl. 4, figs 20–23 ; pl. 9, figs 17–18
 Sahni called these *C.* cf. *carnea*, but they are not mentioned in the text. 27 KCN,
here figured, has cardinalia of a type which very much resembles that of the holotypes
of *Pulchrithyris gracilis* and *C. norvicensis* (Pl. 5, figs 7, 11). 26 KCN has never been
dissected.

Terebratula carnea was the first carneithyridine brachiopod described and strictly
should have been chosen as the type of the genus *Carneithyris*. (Instead, *C.
subpentagonalis* was chosen.) The lectotype and 'syntype' are also from known
localities, in contrast to the types of *C. subpentagonalis*. The three specimens of *C.
carnea* with known localities are possibly from high Beeston Chalk (the types) and

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[1] The use of the term 'Plesiotype' is to be discouraged. It has been used in a variety of senses (Frizzell
1933 : 662; Fernald 1939 : 699), all of them unnecessary. Sahni did not define his use of the term.

Paramoudra Chalk (B 51289) ; this agrees well with their rather small size and thin shells.

Carneithyris elongata (J. de C. Sowerby, 1823)

Pl. 2, figs 1–3 ; Pl. 4, fig. 5

Lectotype : B 49823 (Sowerby) 'Trowse' (Pl. 2, figs 1a–c)
  Sowerby, 1823 : 49 ; pl. 435, fig. 1
  Sahni, 1929 : 32 ; pl. 6, fig. 19
Paralectotype ('Syntype' of Sahni) : B 49824 (Sowerby) 'Trowse' (Pl. 2, figs 2a–b)
  Sowerby, 1823 : pl. 435, fig. 2
  Sahni, 1929 : 32
'Plesiotype' of Sahni : B 45243 (Muir-Wood) 'Catton Pit, north of Norwich' (Pl. 4,
    fig. 5)
  Sahni, 1929 : pl. 4, figs 24–26 ; pl. 10, fig. 9
Others : B 6101 (Davidson *ex* Fitch) 'Upper Chalk, Norwich' (Pl. 2, figs 3a–c)
  Davidson, 1854 : pl. 8, fig. 3

The lectotype and syntype are both from Trowse, possibly the same locality which yielded the types of *C. carnea*. Both specimens are small and rather thin-shelled (Pl. 2, figs 1, 2). The 'plesiotype' might be from high Weybourne Chalk, the Catton Sponge Bed, or low Beeston Chalk. Sahni did not mention the specimen figured by Davidson which I have added here. Incidentally, Norwich Castle Museum also claims that its specimen no. 2072 is the one which Davidson figured ; it is nearly identical to the London specimen but, according to Davidson's own label, there can be no doubt that B 6101 is the one which is figured. The cardinalia of the 'plesiotype' closely resemble those of the 'plesiotype' of *C. carnea* (Pl. 3, fig. 3) and of the paratype B 45604 of *C. circularis* (Pl. 4, fig. 7).

Carneithyris subpentagonalis Sahni, 1925

Pl. 7, figs 2, 3

Holotype : 8 KCN 'Upper Chalk, Norwich' (Pl. 7, fig. 2)
  Sahni, 1925 : 365 ; pl. 23, fig. 15 ; pl. 24, fig. 13 ; pl. 25, fig. 3
  Sahni, 1925a : 498 ; pl. 25, fig. 1
  Sahni, 1929 : 31 ; pl. 5, figs 30, 31 ; pl. 9, figs 5, 6
Paratype : GSM 44491 'Norwich' (Pl. 7, fig. 3)
  Sahni, 1925 : pl. 24, fig. 2 ; pl. 26, fig. 3
  Sahni, 1925a : pl. 25, fig. 7
  Sahni, 1929 : pl. 9, fig. 7
Others : Davidson, 1854 : pl. 8, fig. 2 (Sahni (1925, 1929) considered this figure to
    represent the species, but the original specimen seems to be lost)
  Sahni, 1925a : pl. 25, figs 3–5, 8 (not 9–11 as stated by Sahni)

When Sahni erected *Carneithyris* in 1925 he chose this species as type.   In the collections today it is only represented by the two type specimens ; the specimens representing the ontogenetic Stages I–III of *C. subpentagonalis* (1925a : Pl. 25, figs 3–5, 8) have not been identified.

Carneithyris circularis Sahni, 1925
Pl. 3, figs 1, 2 ; Pl. 4, figs 6, 7

Holotype : 15 KCN 'Norwich' (Pl. 4, fig. 6)
    Sahni, 1925 : 365 ; pl. 24, fig. 14
    Sahni, 1929 : 33
Paratypes : B 49862 (Davidson) 'Norwich' (Pl. 3, fig. 1)
    Davidson, 1854 : pl. 8, fig. 5
    Sahni, 1929 : pl. 5, figs 11–13
      B 45602 (Bayfield) 'Norwich'
    Sahni, 1929 : pl. 5, figs 8–10
      B 45603 (Bayfield) 'Norwich' (Pl. 3, fig. 2)
    Sahni, 1929 : pl. 9, fig. 23
      B 45604 (Bayfield) 'Norwich' (Pl. 4, fig. 7)
    Sahni, 1929 : pl. 5, figs 6, 7 ; pl. 9, fig. 24

The cardinalia of the holotype have not been previously figured.   They are very similar in morphology to those of the paratype of *C. variabilis* (Pl. 7, fig. 4) and somewhat like those of the paratype of *C. subpentagonalis* (Pl. 7, fig. 3).

Sahni (1929) stressed that this species differed from all other *Carneithyris* in its circular outline, but it shares this feature with the lectotype and the 'plesiotype' of *C. carnea* (p. 326), and the holotype of *Magnithyris magna* (p. 333).

Carneithyris variabilis Sahni, 1925
Pl. 5, fig. 1 ; Pl. 7, fig. 4

Holotype : 14 CMN 'Chalk near Norwich' (Pl. 5, fig. 1)
    Sahni, 1925 : 366
    Sahni, 1929 : 34
Paratype : 13 CMN 'Chalk near Norwich' (Pl. 7, fig. 4)
    Sahni, 1925 : pl. 25, fig. 4
    Sahni, 1925a : pl. 25, fig. 2
    Sahni, 1929 : pl. 4, fig. 27

The holotype shows the cardinalia which are not completely dissected out ; they are somewhat similar to those of the holotypes of *C. acuminata* (Pl. 5, fig. 3) and *C. daviesi* (Pl. 6, fig. 3), and of the two possible paratypes of *C. norvicensis*, B 52067 and B 45610 (Pl. 5, fig. 8 ; Pl. 6, fig. 5).   The cardinalia of the paratype closely resemble those of the holotype of *C. circularis* (Pl. 4, fig. 6) and of the paratype of *C. subpentagonalis* (Pl. 7, fig. 3).   While the outer shape of the paratype is very

much like the holotype of *C. subpentagonalis*, Sahni (1925 : 366) stressed that *C. variabilis* had its symphytium hidden under the strongly incurved beak. He (1925a) considered *C. variabilis* as having reached a level of development between his Stages III and IV.

Carneithyris acuminata Sahni, 1925
Pl. 5, fig. 3

Holotype : 19 CMN 'Upper Chalk, Norwich'
  Sahni, 1925 : 366 ; pl. 26, fig. 5
  Sahni, 1929 : 33 ; pl. 5, figs 17–19 ; pl. 9, fig. 15

This species is represented by a single specimen. According to Sahni (1929 : 33) it is distinguished from *C. elongata* by having a 'very much more advanced' cardinal process. However, the only type-specimen of *C. elongata* in which the cardinal process is clearly visible is the 'plesiotype' (Pl. 4, fig. 5) and in this the process would appear to be at least as 'advanced' (in Sahni's terms) as that of *C. acuminata*. Furthermore, the cardinal process of *Ornithothyris carinata* (Pl. 5, fig. 2) is also comparable in morphology.

Carneithyris norvicensis Sahni, 1925
Pl. 5, figs 8, 11 ; Pl. 6, fig. 5 ; Text-fig. 2C

Holotype : GSM 44494 'Norwich' (Pl. 5, fig. 11)
  Sahni, 1925 : 367 ; pl. 24, fig. 5 ; pl. 26, fig. 1
  Sahni, 1929 : 34 ; pl. 4, fig. 29
  It is not known from which pit the holotype was collected.

Paratypes : ? B 52067 'No information' (Pl. 5, fig. 8)
    ? B 45610 (Bayfield) 'Norwich' (Pl. 6, fig. 5 ; Text-fig. 2C)
    ? B 51636 and B 51637 (Sahni) '? Norwich'
  Sahni, 1925 : pl. 26, fig. 14

Sahni (1925 : 367) considered this species distinct, with its vascular markings 'arising from in between the muscle-marks (instead of from their anterior apices), and forking as it were from the pseudoseptum'. Pl. 5, fig. 11 and Sahni (1925 ; pl. 24, fig. 5) show that what he interpreted as 'mantle impressions' are in reality slight depressions on either side of the ridges that form the anterior prolongation of Sahni's 'pseudoseptum' ; they represent a characteristic gerontic feature, like the pitted callus deposits round the bases of the inner socket ridges. It is now impossible to state which of the four specimens identified as *C. norvicensis* is the paratype figured, but not mentioned, in 1925. Both those here figured have large, swollen cardinal processes : the cardinalia of this nominal species are shown here for the first time. B 51636 and B 51637 are probably from Attoe's pit, Catton (see p. 324). The first of these two was originally about 42 mm long and has a somewhat thickened posterior end ; the other has very strong callus deposits in the posterior part of the valves, so much so that the cardinalia seem to sit astride a cushion.

Carneithyris subovalis Sahni, 1925a
Pl. 4, figs 3, 4 ; Text-fig. 2A

Holotype : B 15159 (Bayfield) 'Norwich' (Pl. 4, fig. 3 ; Text-fig. 2A)
  ? Sahni, 1925a : 500 ; pl. 25, fig. 10 (not 4 or 5 as stated by Sahni)
  Sahni, 1929 : 34 ; pl. 4, fig. 33 ; pl. 9, fig. 16
Paratype : Norwich Castle Museum (no number) 'Upper Chalk, Norwich' (Pl. 4, fig. 4)
  Sahni, 1929 : pl. 4, figs 31, 32 ; pl. 10, fig. 17
  ? Sahni, 1925a : pl. 25, fig. 11 (not 4 or 5 as stated by Sahni)
Others : B 45659 (C. Birley) 'Norwich' (identified and dissected by Sahni)
  B 15157 (Bayfield) 'Norwich' (called 'young specimen' by Sahni)
  B 45652 (Bayfield) 'Norwich' (called *C. subovalis* (?) by Sahni)
  B 44182 (Rowe) 'Edward's Pit (now Campling's) Mousehold' (identified by Sahni)
  B 51274 (Rowe) 'Mousehold' (identified by Sahni, *not* identical with the specimen figured in 1958 with the same number, see p. 326)

None of the three specimens which were opened and dissected by Sahni resemble either of the two specimens said to represent the species in his pl. 25, figs 4, 5.   On the other hand, the holotype and the paratype look much more like his pl. 25, figs 10, 11, and it would seem that the figures have been mistakenly interchanged, as in pl. 25, fig. 9.

This species is considered to represent Stages I–II in the evolutionary tree.   The two unopened specimens from Rowe's collection came from Mousehold Pit (= Magdalen Chapel) and the three specimens from Bayfield's collection might have come from the same.   Thus, at least five of the specimens seem to have come from the upper low Beeston Chalk, which is known for its large brachiopods.

Carneithyris uniplicata Sahni, 1925a
Pl. 4, fig. 9

Holotype : GSM 48518 'Thorpe' (Pl. 4, fig. 9)
  Sahni, 1925a : 500 ; pl. 25, fig. 6
  Sahni, 1929 : 35 ; pl. 4, fig. 30 ; pl. 10, fig. 18
Others : GSM 48514 and 48515 'Whitlingham' (brachial and pedicle valve of the same specimen identified by Sahni as *C.* cf. *uniplicata*)

In his original description of this species Sahni (1925a : 500) stressed 'the primordial character' of its cardinal process and made it the representative of his Stage I in his evolutionary tree of cardinal processes (see p. 322).   This, however, does not fit very well with the provenance of the material, which is from late Beeston Chalk to Paramoudra Chalk.   The incipient plication which is discussed on p. 361 also supports the late age.

Carneithyris daviesi Sahni, 1925a

Pl. 6, figs 1–4 ; Pl. 7, fig. 1 and Text-fig. 2D

Holotype : B 45599 (Bayfield) 'Norwich' (Pl. 6, fig. 3)
  Sahni, 1925a : 500 ; pl. 25, fig. 9 (not 3 as stated by Sahni)
  Sahni, 1929 : 36 ; pl. 9, fig. 10
Paratype : B 459 (Bayfield) 'Norwich' (Pl. 6, figs 1, 2 ; Pl. 7, fig. 1 ; Text-fig. 2D)
  Sahni, 1929 : pl. 5, figs 4, 5 ; ? pl. 9, fig. 8 ; pl. 9, fig. 9
Others : B 45642 (C. F. Cockburn) 'Norwich' (identified and dissected by Sahni)
    (Pl. 6, fig. 4)

The two type specimens are the largest and most gerontic carneithyridines in the Bayfield collection. The paratype shows particularly extreme gerontic features : Pl. 6, fig. 1 and Pl. 7, fig. 1 show the swollen and protruding cardinal process and the thickened hinge region of the brachial valve in this specimen. The pedicle valve, moreover, shows the most gerontic features to be seen in any *Carneithyris* in the British collections (Pl. 6, figs 1, 2) ; the enormously thickened tooth bases overlap but have not fused and a tube is left open for the pedicle case and its muscles. There is a 'pearl' in the adductor muscle impression. The length of the pedicle valve is 43 mm. The 'drawing of the brachial valve of a large specimen with brachidium' (Sahni 1929 : pl. 9, fig. 8) has a remarkable resemblance to the paratype, when the brachial valve of this is tilted slightly.

The holotype (Pl. 6, fig. 3) also exhibits a swollen cardinal process and has some callus deposits in the posterior part of the valves. The length of the pedicle valve was c. 35·5 mm. The third specimen, B 45642, was not completely dissected by Sahni, but nevertheless shows a cardinal process very much like that of the holotype ; it is fairly thin-shelled and is only about 33 mm long.

C. daviesi was considered to represent Stage III in the evolution of cardinal processes (Sahni 1925a).

Carneithyris ornata Sahni, 1929

Pl. 4, figs 11, 12

Holotype : GSM 48498 'Thorpe'
  Sahni, 1929 : 35 ; pl. 4, fig. 28 ; pl. 10, fig. 22

The nominal species is represented by a single specimen, in which, apart from the preserved original colour pattern, Sahni (1929 : 35) found 'a small septum in the pedicle valve' and unusually shaped vascular markings. There is a slight ridge between the ventral adjustor scars and the vascular markings are clear ; these, in connection with the pitted callus deposits in the posterior part of the valves (Pl. 4, fig. 12), are gerontic features of this particular specimen.

Pulchrithyris gracilis Sahni, 1925

Pl. 5, figs 4–7

Holotype : GSM 48487 'Magdalen Chapel, Norwich' (Pl. 5, fig. 7)
    Sahni, 1925 : 362 ; pl. 23, fig. 6 ; pl. 24, fig. 12a
    Sahni, 1929 : 36 ; pl. 5, figs 26–28 ; pl. 9, fig. 11
Paratype : GSM 48485 'Harford Bridges' (Pl. 5, fig. 6)
    Sahni, 1925 : pl. 24, fig. 12
    Sahni, 1929 : pl. 9, fig. 13
Others : B 46300 (Muir-Wood) 'Catton Pit, Norwich' (Pl. 5, fig. 5)
    Sahni, 1929 : pl. 9, fig. 12
      B 98123 (J. Brown) 'Charing, Kent' (Pl. 5, fig. 4)
    Sahni, 1929 : pl. 9, fig. 14
      B 51492 (Rowe) 'Thorpe, Limekiln Pit'
    Sahni, 1958 : 16 ; pl. 6, figs 7a–c
      B 51271–51273 (Rowe) 'Mousehold'
      B 51275, 51276 (Rowe) 'Whitlingham'
      B 51277 (Rowe) 'Mousehold'
      B 51278 (Rowe) 'Whitlingham'
      B 51279–51281 (Rowe) 'Mousehold'
      B 51282 (Rowe) 'Whitlingham'
      B 51283, 51284 (Rowe) 'Mousehold'
      B 51285 (Rowe) 'Whitlingham'
      B 51286, 51287 (Rowe) 'Mousehold'
    Sahni 1958 : 16 (B 51271–3, B 51275–87 inclusive)
      GSM 48484, 48486 (J. H. Blake) 'Trowse' (identified by Sahni)

When the species was first erected it was intended to cover what some authors had called *Terebratula elongata*.   The genus *Pulchrithyris* was distinguished by having a loop which was 'exceptionally flat, bow-shaped with anteriorly directed apex (a very distinctive feature)' (1925 : 362).   The peculiar loop can also clearly be seen on pl. 23, fig. 6.   Later Sahni made *Pulchrithyris* a synonym of *Carneithyris* ; 'Owing to its delicate character I was unable to obtain the brachial apparatus of these two species without damaging the loop, and this led me into an error as to the orientation of this latter structure in relation to the crura' (Sahni 1929 : 31).   The holotype was now figured with the loop glued on with the correct side up while the loop of the paratype remained upside down, as it does to this day (Pl. 5, fig. 6 ; see Sahni 1929 : pl. 9, fig. 13).

The holotype is from Magdalen Chapel (= Mousehold) ; the label of the paratype gives the locality erroneously as Lollard's pit, Thorpe (high Beeston Chalk), owing to an incorrect transcription of information from the old catalogue.   The actual locality should be Harford Bridges which, according to C. J. Wood (personal communication 1973), comprised at least three pits in the upper third of the Weybourne Chalk.

Sahni (1929) figured two other specimens, one of which according to its label would be from Charing, Kent (Pl. 5, fig. 4). This must be an error, since from its characteristic features and pink colour there is no doubt that it came from an Upper Campanian locality in Norfolk. Later (1958) 17 specimens from Rowe's collection were dealt with. Of these, 11 are from Mousehold (the type locality), five from Whitlingham and one from Thorpe, Limekiln Pit (not Thorpe St Andrew's as stated on the label). Two specimens in the collections of the Institute of Geological Sciences, both from 'Trowse', have been identified by Sahni as belonging to this species. Thus the material of *C. gracilis* covers a stratigraphical range from high Weybourne Chalk to high Paramoudra Chalk. All specimens of the nominal species are rather small in comparison with many of the others, and none of the opened specimens shows extreme gerontic features.

Pulchrithyris extensa Sahni, 1925
Pl. 4, fig. 8

Holotype : 7 KCN 'Upper Chalk, Norwich'
  Sahni, 1925 : 363 ; pl. 24, fig. 15 ; pl. 25, fig. 8 ; pl. 26, fig. 8
  Sahni, 1929 : 36 ; pl. 6, figs 29–31

In its present condition the single specimen has no brachidium. Sahni neither figured nor described its cardinalia and brachidium, so it is difficult to see any reason for placing it in the genus *Pulchrithyris*. Sahni considered it distinct through its 'much elongate and pod-shaped character'. Its cardinal process is slightly asymmetrical but somewhat resembles that of *Carneithyris ornata* (Pl. 4, fig. 12).

Magnithyris magna Sahni, 1925
Pl. 4, fig. 1 ; Pl. 5, fig. 10

Holotype : GSM 48488 'Thorpe' (Pl. 4, fig. 1)
  Sahni, 1925 : 367 ; pl. 23, fig. 1 ; pl. 24, fig. 1 ; pl. 25, fig. 1
  Sahni, 1929 : 39 ; pl. 5, figs 1–3 ; pl. 10, fig. 7
Others : B 15149 (Bayfield) 'Norwich' (Pl. 5, fig. 10)
  Sahni, 1929 : pl. 10, fig. 8
    B 44680, 45609, 45611 (Bayfield) 'Norwich' (identified and dissected by Sahni)
    B 45586 (Bayfield) 'Norwich' (called 'young' by Sahni)
    B 45639 (C. F. Cockburn) 'Norwich' (identified and dissected by Sahni)

The genus *Magnithyris* is said to be distinct from *Carneithyris* in 'its peculiar obtuse beak, its distinctive cardinal process and brachidium. The foramen . . . is also much larger than in species of *Carneithyris*, and the socket-ridges very much thinner' (Sahni, 1929 : 39). Pl. 4, fig. 1 shows the cardinalia, which somewhat resemble those of *M. truncata* (Pl. 4, fig. 2).

The other figured specimen B 15149 has less feeble cardinalia than the holotype but the transverse band, which is broken off, is concealed in matrix and the left crus is

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glued on in the wrong position.   The diameter of the pedicle foramen is 1·2 mm, but several of the types of *Carneithyris* spp. have foramina of this order of size, e.g. *C. circularis* (paratype B 49862), *C. daviesi* (paratype) and *Ellipsothyris similis* (holotype).   Sahni (1929 : 38) erroneously called this specimen a paratype of *Ellipsothyris similis* (see p. 335).

B 44680, 45609, 45611 have been dissected ; none of them shows particularly thin socket ridges and the diameters of the pedicle foramina do not exceed 1·5 mm. B 45586 has not been opened ; its pedicle valve is 29 mm long and its foramen is 1·0 mm in diameter.   B 45639 has cardinalia closely resembling those of *M. truncata* (Pl. 4, fig. 2).   This type of *Carneithyris* is discussed further on p. 360.

Magnithyris truncata Sahni, 1929
Pl. 4, fig. 2

Holotype : B 45606 (Bayfield) 'Norwich'
  Sahni, 1929 : 39 ; pl. 5, figs 14–16 ; pl. 10, fig. 6
  This species is represented by a single specimen ; its shell is thin and transparent, the cardinalia are likewise very delicate and the foramen is large and labiate.   For further discussion of this extreme variant of *Carneithyris* see p. 360.

Piarothyris rotunda Sahni, 1925
Pl. 3, fig. 4

Holotype : 18 KCN 'Upper Chalk Norwich'
  Sahni, 1925 : 370 ; pl. 23, fig. 14 ; pl. 24, fig. 11 ; pl. 25, fig. 6 ; pl. 26, figs 6, 12
  Sahni, 1929 : 37 ; pl. 5, figs 23–25 ; pl. 10, fig. 20
  This single specimen, on which the genus *Piarothyris* was founded, was considered a *Carneithyris* by Muir-Wood (1965 : 799).   However, it possesses all the characteristics of a *Gibbithyris*.   The figure shows the feeble, transverse cardinal process, the ventrally convex hinge-plates and the dorsally directed crura bases.   To judge from its external characters, the specimen may have come from a horizon rich in brachiopods in the upper part of the *Micraster coranguinum* Zone (Santonian) in south-east England (C. J. Wood, personal communication 1970).   A tiny sample of chalk matrix was taken from the cardinalia, but an analysis of the coccoliths in it by Dr K. Perch-Nielsen of Copenhagen revealed only undiagnostic, long-ranged forms.

Ellipsothyris similis Sahni, 1925
Pl. 4, fig. 10 ; Pl. 7, fig. 5 and Text-fig. 2E

Holotype : 14 KCN 'Upper Chalk Norwich' (Pl. 4, fig. 10)
  Sahni, 1925 : 371 ; pl. 23, fig. 13 ; pl. 24, fig. 8 ; pl. 25, fig. 9
  Sahni, 1929 : 38 ; pl. 6, figs 12–15 ; pl. 9, fig. 22

? Paratype : B 45653 (Bayfield) 'Norwich' (Pl. 7, fig. 5 ; Text-fig. 2E)
  Sahni 1929 : pl. 9, fig. 1 (in the text, p. 38, B 15149 is said to be a paratype, but
    this specimen is figured on pl. 10, fig. 8 as *Magnithyris magna*)
Others : B 45629 (J. F. Walker) 'Norwich' (identified and dissected by Sahni)

The genus *Ellipsothyris* is based on the cardinal process being 'ellipsoidal with
flat dorsal surface, bearing two very incipient knobs postero-laterally and a median
one' and the brachidium being 'narrow posteriorly, comparatively broad anteriorly'.
The type of cardinal process (Pl. 4, fig. 10) is very similar to that of *Carneithyris
circularis* (B 45604, Pl. 4, fig. 7). The brachidium of the holotype is only partly
dissected out of the chalk matrix and is now detached from the valve ; its apparent
shape in Sahni's illustration (1929 : pl. 9, fig. 22) is mainly due to retouching of the
photograph. The presumed paratype differs markedly from the holotype, having
completely fused *Chatwinothyris*-like cardinalia and a fairly parallel-sided brachidium
(Pl. 7, fig. 5 and Text-fig. 2E). The third identified specimen has cardinalia of a
more swollen type than those of the holotype.

Ornithothyris carinata Sahni, 1925

Pl. 5, fig. 2

Holotype : 17 KCN 'Upper Chalk Norwich'
  Sahni, 1925 : 374 ; pl. 23, fig. 2 ; pl. 24, fig. 6 ; pl. 25, fig. 5
  Sahni, 1929 : 44 ; pl. 6, figs 27, 28 ; pl. 10, fig. 19

The genus and species are represented by a single specimen. Sahni stressed the
importance of the 'conspicuous carination of its ventral valve, which points to a
sulcate ancestry' and of the transverse band of the brachidium which 'shows a
sudden arching up in the middle, producing a slight break in the curve and forming
as it were a sub-arch' (Sahni 1925 : 374 ; 1929 : 44). However, Sahni's illustration
(1929 : pl. 6, fig. 28) does not show any conspicuous carination of the pedicle valve,
and I was unable to see it on the remains of the specimen. The 'sub-arch' on the
loop is no more accentuated than in other terebratulids, so far as can be seen, since
the brachidium is partly covered by matrix (Pl. 5, fig. 2). In shape and preservation
the cardinalia are practically identical with those of *C. acuminata* (Pl. 5, fig. 3).

Chatwinothyris subcardinalis Sahni, 1925

Pl. 8, figs 1–4

Holotype : GSM 44501 (C. Reid) 'Trimingham Foreshore, *O. vesicularis* Bed' (Pl. 8,
    fig. 1)
  Sahni, 1925 : 369 ; pl. 23, fig. 9 ; pl. 24, fig. 4a ; pl. 26, fig. 4
  Sahni, 1925a : 499 ; pl. 25, fig. 12
  Sahni, 1929 : 40 ; pl. 5, figs 20–22 ; pl. 10, fig. 4
Paratype : B 46326 (A. Laur) 'Isle of Rügen, Germany' (Pl. 8, fig. 2)
  Sahni, 1925 : pl. 24, fig. 4
  Sahni, 1929 : pl. 6, figs 10–12 ; pl. 10, fig. 1

Others : B 46327 and B 21266 (A. Laur) 'Isle of Rügen, Germany' (Pl. 8, figs 3, 4)
    Sahni, 1929 : pl. 10, figs 2, 3
      B 51046, 51049 (Rowe) 'Trimingham, *lunata* reef'
    Sahni, 1958 : 15 ; pl. 5, figs 1a–c, 2a–c
      B 51087, 51058 (Rowe) 'Trimingham, "non-*lunata*" reef'
    Sahni, 1958 : pl. 5, figs 3, 4
      B 51060 (Rowe) 'Trimingham' (not present in the collection)
    Sahni, 1958 : pl. 5, fig. 4x

The holotype is presumably from the lower part of the Grey Beds (C. J. Wood, personal communication 1972) while the paratype and the two other specimens figured in 1929 are from the Isle of Rügen, north Germany (*Belemnella occidentalis* Zone). Sahni (1958 : 15) mentioned that there were 'over fifty specimens' in Rowe's collection ; the specimens figured in 1958 were all from the Trimingham foreshore, from '*Ostrea lunata*' Beds and Grey Beds (see p. 325).

The genus *Chatwinothyris*, of which *Ch. subcardinalis* is the type, is distinguished from *Carneithyris* by having indistinct beak ridges and a pin-hole foramen.   Furthermore, 'in *Carneithyris* there is no tendency towards fusion of cardinalia, which is an important feature of *Chatwinothyris*' (Sahni, 1929 : 40).

As can be seen from the figures, this species was permitted unusual freedom of variation in internal characters by its author.   The cardinalia of the holotype and B 21266 (Pl. 8, figs 1, 4) show hardly any fusion (compare Popiel-Barczyk 1968 : pl. 9, fig. 1 ; pl. 3, fig. 5).   The paratype (Pl. 8, fig. 2) has completely fused cardinalia and looks much like the specimens figured by Steinich (1965 : text-fig. 27(3)) from the Lower Maastrichtian of Rügen and by Popiel-Barczyk (1968 : pl. 8, fig. 7) from the Upper Maastrichtian of Poland.   The paratype of *Ch. subcardinalis* is not quite as advanced in its fusion as the holotype of *Ch. curiosa* (Pl. 8, fig. 5).   B 46327 (Pl. 8, fig. 3) has nearly completely fused cardinalia, though not to the degree of those of the paratype, and the flaps on the sides of the diductor muscle scars have united to form tubes which surrounded the posterior part of the diductor muscles. A similar development is shown by the specimen figured by Steinich (1965 : text-fig. 27(4)).   Popiel-Barczyk (1968 : pl. 5, fig. 6) illustrated under the name *Carneithyris carnea* another specimen showing this development, and in pl. 9, fig. 3, a more gerontic specimen of *Ch. subcardinalis*, both from the Upper Maastrichtian of Poland.

Chatwinothyris symphytica Sahni, 1925

Pl. 2, fig. 4 and Text-fig. 2F

Holotype : GSM 47523 'Chalk near Norwich'
    Sahni, 1925 : 369 ; pl. 23, fig. 7 ; pl. 24, fig. 7 ; pl. 26, fig. 9
    Sahni, 1929 : 42 ; pl. 10, fig. 13 (called *Ch.* (?) *symphytica* in the text to the figure)

This single specimen shows no tendency to a fusion of the cardinalia, which should be the main feature separating *Chatwinothyris* from *Carneithyris*. Sahni (1925, 1929) himself mentioned this, but for reasons unknown preferred to retain this

specimen in *Chatwinothyris*. The specimen is gerontic, with pitted callus deposits in the posterior part of the valves, and the extreme development of the cardinal process can be taken to be a result of old age as in the holotype and paratype of *Carneithyris daviesi* (Pl. 6, fig. 3 ; Pl. 7, fig. 1).

Chatwinothyris curiosa Sahni, 1925a

Pl. 8, fig. 5

Holotype : B 45669 (Savin) 'Trimingham, Zone of *Ostrea lunata*'
    Sahni, 1925a : 499 ; pl. 25, fig. 13
    Sahni, 1929 : 43 ; pl. 6, fig. 26 ; pl. 10, fig. 12
    Sahni, 1958 : 15 ; text-fig. 3

The original description (1925a : 499) reads as follows : 'Here the socket-ridges and the crural bases are somewhat more developed and the process of fusion has gone a step further, so much so that no trace whatever is left of the cardinal process. Its position is now occupied by a narrow flat platform bounded laterally by the partially overhanging and fused crural bases and socket-ridges. Hence it follows that the diductor muscles, in this case, would be attached to this platform instead of directly to the cardinal process, and that the partial articulatory function of the latter has been assumed by the cardinalia.' The specimen figured in pl. 25, fig. 13 has no loop and apparently a gaping hole where the cardinal process should have been. In 1929 (pl. 10, fig. 12) a transverse band has curiously appeared which shows a striking colour difference from the cardinalia. The species was discussed again by Sahni (1958 : 15) under the genus *Chatwinothyris* : 'The cardinal process in such forms becomes atrophied and its function is relegated, partly at any rate, to the fused cardinalia. In extreme cases the cardinal process becomes almost completely resorbed, e.g. in *Chatw. curiosa*.'

An examination of the holotype showed that the gaping black hole on the 1925 illustration was in fact white chalk completely filling the space between the diductor muscle attachment area and the umbo of the valve. When this chalk was removed the diductor impressions could be seen (Pl. 8, figs 5a, b). The curious transverse band is glued onto the interior sides of the crura and thus does not fit this specimen, but must have been derived from a smaller one (Pl. 8, figs 5c, d). Furthermore, this transverse band has the pinkish colour typical of Campanian *Carneithyris* while the rest of the valve is of the greyish colour typical of beekitized Maastrichtian specimens. Specimens with completely fused cardinalia like the holotype are not uncommon in the Maastrichtian (e.g. Nielsen 1909 : pl. 2, figs 71, 75 ; Steinich 1965 : 43, figs 27(3), 32 ; Popiel-Barczyk 1968 : text-fig. 12, pl. 10, figs 1–5). Furthermore, both the paratype of *Chatwinothyris subcardinalis* and the paratype of *Ellipsothyris similis* belong to this type. The tendency towards a complete obliteration of the boundaries between the different elements in the cardinalia is very strong in the Maastrichtian specimens as a result of the general thickening of the posterior part of the shell. Growth studies (Steinich 1965 : text-figs 27 and 29–31) and cellulose peels of serial sections show that a gradual fusion of the cardinalia takes place and it is not a case

of suppression or even resorption of the cardinal process as postulated by Sahni. (It is intended to publish serial sections of *Carneithyris* from the Danish Maastrichtian and Danian in a later study now under preparation.)   I therefore see no reason to consider B 45669 as representing a separate species, but take it to be well within the variation of *Carneithyris subcardinalis*.

Chatwinothyris gibbosa Sahni, 1925a

Pl. 1, fig. 4

Holotype : B 45670 (Savin) 'Trimingham, Zone of *Ostrea lunata*'
    Sahni, 1925a : 499 ; pl. 25, fig. 14
    Sahni, 1929 : 43 ; pl. 5, figs 32, 33 ; pl. 10, fig. 21

In the original description (1925a : 499) Sahni pointed out that in *Ch. gibbosa* 'the degree of development and fusion reached by the hinge-parts is about the same as in *C. subcardinalis*, but the former species can be easily distinguished from the latter by its marked gibbous shell and mesothyrid foramen'.   As can be seen from 1929 : pl. 5, fig. 33, the valves are gaping and this has added c. 1·5 mm to the thickness.   In his generic diagnosis Sahni (1929 : 40) wrote 'beak-ridges feeble, so that it is impossible satisfactorily to define the position of the foramen with regard to these'.   I consider that the position of a pin-hole foramen relative to beak ridges which are at best very indistinct and in most cases missing entirely is a character of no specific value.

The specimen is considered to fall well within the variation of *Carneithyris subcardinalis*.

V. DISCUSSION

Studies of living and fossil communities of brachiopods have shown that several species of the same genus can co-exist in the same environment.   For example, in the Caribbean Sea off Barbados, three species of *Argyrotheca* can be found attached to the same sponge (unpublished observation).   Similarly, three closely related genera of micromorphic cancellothyridines represented by five species adapted to the same mode of life occur in the Maastrichtian white chalk of Denmark (Surlyk 1972).

On the other hand, it is not easy to accept that six closely related genera represented by 18 species could have existed in the Upper Campanian sea of the Norwich area, of which at least nine species probably occur together at the same horizon in the Beeston Chalk.   This high degree of apparent speciation in an environment offering a rather limited variety of ecological niches appears to be taxonomic rather than ecological and to be due to excessive 'splitting'.

The six genera of carneithyridines, represented by 18 species, were erected by Sahni on the basis of about 55 specimens in museum collections.   Because of this limited material it is very difficult to identify any new material with the original type series.   Sahni allowed single species little freedom of variation and his diagnoses were based on minor differences in outline of the shells, the size of the pedicle foramen,

the curvature of the beak and the development of beak ridges.   Small differences in the shape of the muscle impressions and cardinalia were also considered important.

Thus, with new material at hand, the student of carneithyridines has one of two courses open to him.   Either he must continue to attempt to split the group up on the basis of Sahni's species characters, or he must combine some of the existing genera and species in order to create broader species which can be identified easily and so prove useful to the stratigrapher and field geologist.   On the basis of a study of new material in the English collections and observations in the field I have chosen to follow the latter course.

Material

By 1929, Sahni's studies seem to have been based on about 55 specimens of Campanian carneithyridines.   Since that time the British Museum (Natural History) has come into possession of A. W. Rowe's large collection of *Carneithyris* ;   the Institute of Geological Sciences, London, has profited from C. J. Wood's intensive collecting in the extant exposures of Norfolk chalk ; and the Norwich Castle Museum has obtained R. M. Brydone's collection of Campanian carneithyridines, to which the collections of M. Leader and J. Goff have now been added.

The new material is stratigraphically well zoned.   It has also the advantage that it consists not only of perfect but also of crushed and incomplete specimens, thus offering a good view over the internal and external features and their variation. This contrasts with the general attitude of collectors in the 19th century which led to the selection of very large, perfect specimens.   There was consequently an unintentional bias towards the gerontic end of the spectrum of variation.

Fig. 1 shows the material used in this chapter.   An attempt has been made to list the localities in stratigraphical order while the columns in mutual contact signify localities considered to be of the same age or with stratigraphical overlap.   The figure also aims to give a visual impression of the quantitative distribution of the material.   Altogether 214 specimens have been measured for a statistical analysis of the external characters.

Campanian carneithyridines so far have been found only in chalk ranging from the upper third of the Weybourne Chalk to the top of the Paramoudra Chalk ; according to Peake & Hancock (1961) this comprises about 55 m of chalk.   The material from Bramerton is included here with the Campanian specimens because it has 'Campanian' cardinalia and colouration, in contrast to the Maastrichtian *Carneithyris subcardinalis*.   But according to C. J. Wood (personal communication 1972), Bramerton is of Maastrichtian age although the small exposure in the riverbank has so far yielded only *Belemnitella* and no *Belemnella*.

The phylogenetic tree of Sahni (1925a)

According to Sahni (1925a : 498) this 'tree', in combination with Stages I to IV of the ontogeny of the cardinalia in *C. subpentagonalis*, 'confirms the dictum that Ontogeny repeats Phylogeny' (see p. 322).   However, the provenance of the individual species of the tree suggests that the stratigraphical order in which they have been placed may be questioned.
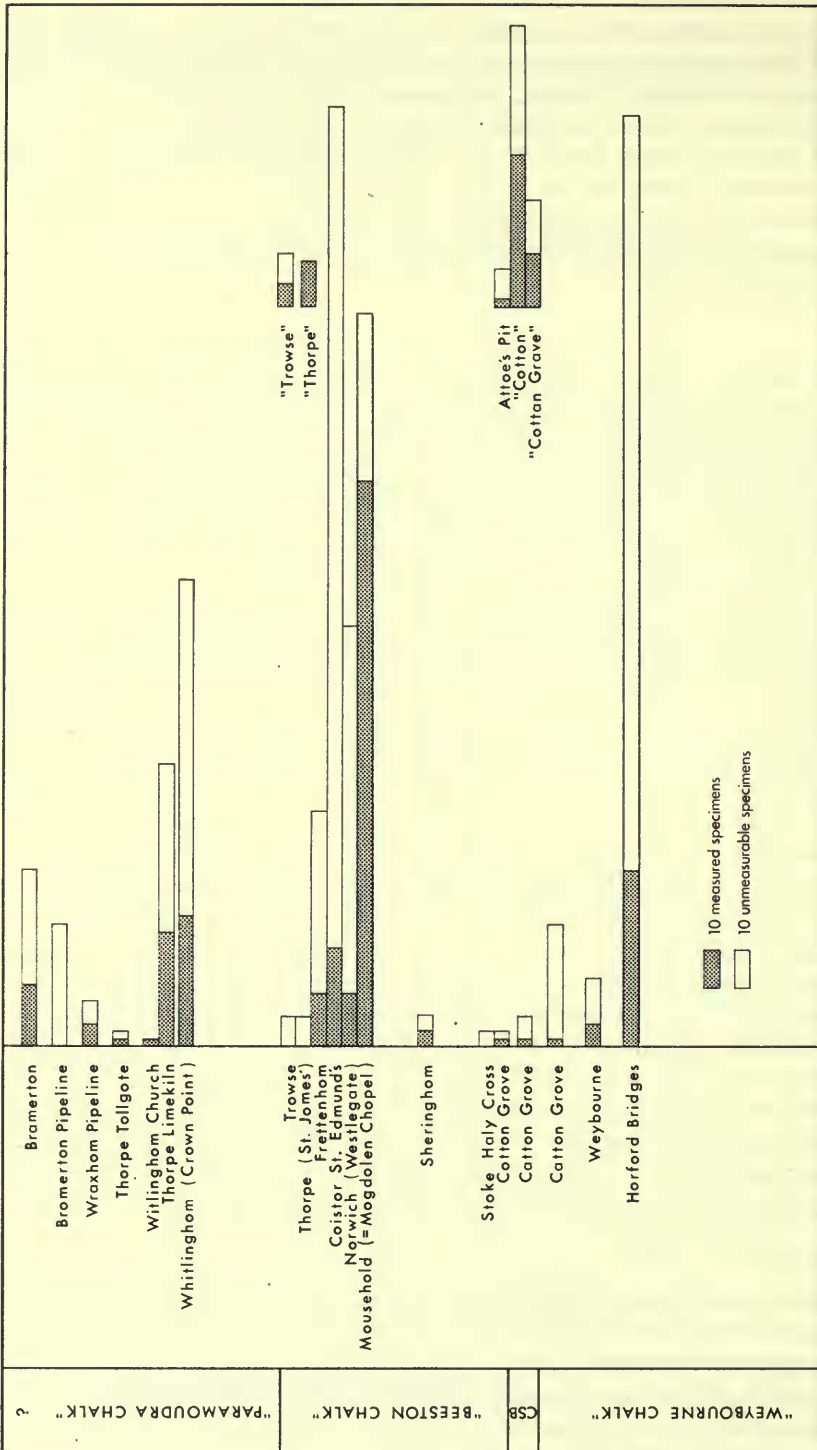
Fig. 1.   Stratigraphical distribution of the material.   Shaded columns represent measured specimens, white columns unmeasurable
specimens.   5 mm = 10 specimens.

Carneithyris uniplicata was placed at the root of the tree. As mentioned on p. 330, however, the holotype is from high Beeston Chalk or high Paramoudra Chalk and the other specimen is from high Paramoudra Chalk. At least five of the seven known specimens of *C. subovalis* probably came from low Beeston Chalk. One of the three known specimens of *C. daviesi* is extremely gerontic and the two types are supposed to be from low Beeston Chalk. *C. variabilis* is represented by two specimens from the old collections of Norwich Castle Museum and are therefore unlocalized. The crown of the tree is *C. subpentagonalis* but it is not known from which horizons the two types came. The three unlocated specimens of this species figured by Sahni (1925a : pl. 25, figs 3–5 and 8) may be in his private collection and may therefore have come from Attoe's Pit, Catton (p. 324) ; they may thus be from highest Weybourne Chalk, the Catton Sponge Bed or low Beeston Chalk. It is thus clear that the species chosen by Sahni cannot represent a phylogenetic lineage.

Morphology of the cardinalia

Fig. 2 illustrates the six different types of cardinalia met with in the Upper Campanian carneithyridines. In Table 1, Sahni's figured specimens and those which he dissected and identified to species have been grouped according to type of
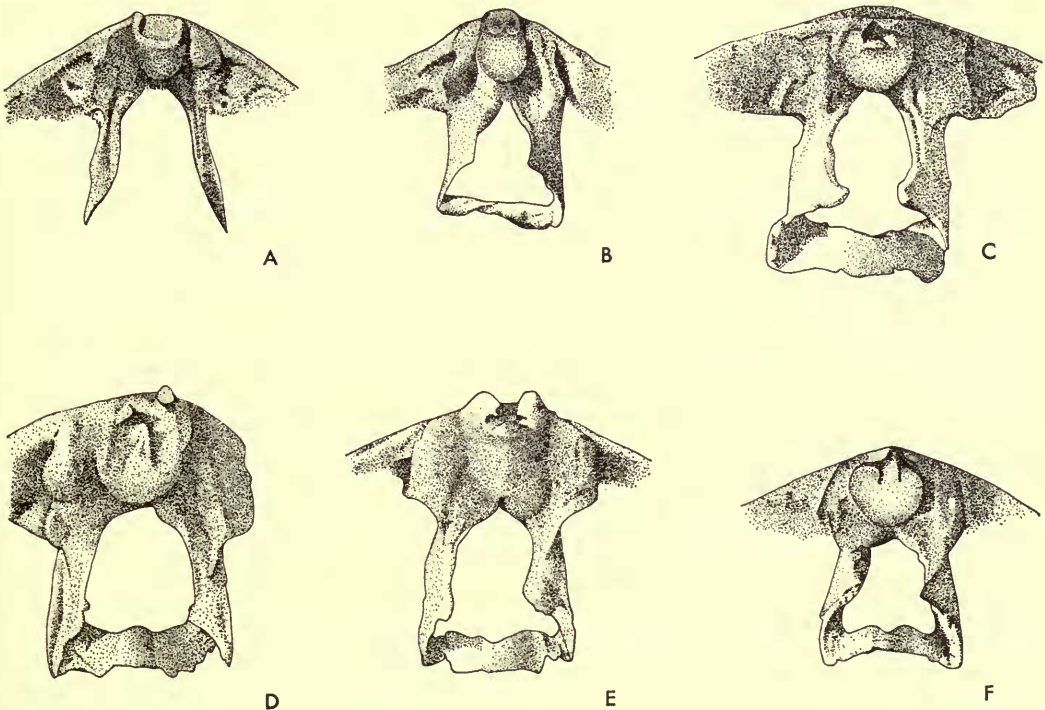
FIG. 2. Six different types of cardinalia in *Carneithyris*. A : *C. subovalis*, holotype ; B : *C.* cf. *carnea*, 27 KCN ; C : *C. norvicensis*, B 45610 ; D : *C. daviesi*, paratype ; E : *Ellipsothyris similis*, ? paratype ; F : *Chatwinothyris symphytica*, holotype.

TABLE I

Sahni's specimens grouped according to the type of cardinalia

TYPE A : Slender, conical to hemispherical cardinal process with or without ridges or flaps
between or around the diductor impressions ; socket ridges and crural bases not thickened.

Carneithyris subovalis, holotype B 15159 (Fig. 2A ; Pl. 4, fig. 3) ; unnumbered paratype (Pl. 4,
fig. 4)

C. carnea, 'plesiotype' B 45600 (Pl. 3, fig. 3)

C. elongata, paralectotype B 49824 (Pl. 2, fig. 2) ; 'plesiotype' B 45243 (Pl. 4, fig. 5)

C. uniplicata, holotype GSM 48518 (Pl. 4, fig. 9)

C. circularis, holotype 15 KCN (Pl. 4, fig. 6) ; paratypes B 45603, B 45604 (Pl. 3, fig. 2 ; Pl. 4,
fig. 7)

C. ornata, holotype GSM 48498 (Pl. 4, fig. 12)

Pulchrithyris extensa, holotype 7 KCN (Pl. 4, fig. 8)

Ellipsothyris similis, holotype 14 KCN (Pl. 4, fig. 10)

Magnithyris magna, holotype GSM 48488 (Pl. 4, fig. 1)

M. truncata, holotype B 45606 (Pl. 4, fig. 2)

TYPE B : Cardinal process more swollen and protruding than in type A ; socket ridges and
crural bases somewhat thickened.

Carneithyris cf. *carnea*, 27 KCN (Fig. 2B ; Pl. 5, fig. 9)

C. variabilis, holotype 14 CMN (Pl. 5, fig. 1)

C. acuminata, holotype 19 CMN (Pl. 5, fig. 3)

C. norvicensis, holotype GSM 44494 (Pl. 5, fig. 11)

Pulchrithyris gracilis, holotype GSM 48487 (Pl. 5, fig. 7) ; paratype GSM 48485 (Pl. 5, fig. 6) ;
B 46300 (Pl. 5, fig. 5)

Magnithyris magna, ? paratype B 15149 (Pl. 5, fig. 10)

Ornithothyris carinata, holotype 17 KCN (Pl. 5, fig. 2)

TYPE C : Cardinalia intermediate between types B and D ; the specimens large and thick-
shelled.

C. norvicensis, ? paratype B 45610 (Fig. 2C ; Pl. 6, fig. 5) ; ? paratype B 52067 (Pl. 5, fig. 8) ;
B 51636 (not figured)

C. daviesi, holotype B 45599 (Pl. 6, fig. 3) ; B 45642 (Pl. 6, fig. 4)

C. subpentagonalis, paratype GSM 44491 (Pl. 7, fig. 3)

C. variabilis, paratype 13 CMN (Pl. 7, fig. 4)

Pulchrithyris gracilis, B 98123 (Pl. 5, fig. 4)

TYPE D : Cardinalia strongly thickened with extremely swollen and protruding cardinal process
with ridges and flaps.

C. daviesi, paratype B 459 (Fig. 2D ; Pl. 7, fig. 1)

C. subpentagonalis, holotype 8 KCN (Pl. 7, fig. 2)

TYPE E : Swollen, completely fused cardinalia.

Ellipsothyris similis, ? paratype B 45653 (Fig. 2E ; Pl. 7, fig. 5)

TYPE F : Cardinalia strongly thickened and completely dominated by the swollen cardinal
process.

Chatwinothyris symphytica, holotype GSM 47523 (Fig. 2F ; Pl. 2, fig. 4)

Carneithyris norvicensis, B 51637 (not figured)

cardinalia. Comparison of Sahni's material with the new, dissected material in the English collections clearly shows a general tendency in the development of the cardinalia. Types A and B are found in specimens showing no gerontic features. Type C appears in specimens which show incipiently gerontic features such as crowding of growth lines at the frontal margin and callus deposits around the teeth bases and the dental sockets. Type D is common in gerontic specimens while E and F are rarely met with and found only in specimens with extremely gerontic features (e.g. the paratypes of *Carneithyris daviesi* and *Ellipsothyris similis*).

It can furthermore be seen in Table 1 that in some of Sahni's species the specimens in the type series belong to different groups. In most cases, however, Sahni's diagnoses took account of the cardinalia of the holotypes only, as e.g. in *E. similis*.

The large numbers at hand demonstrate that the cardinalia of the carneithyridines are subject to great variation, which is dependent on the ontogenetic age of the single individual and not on its geological age. From the upper part of the Weybourne Chalk to the top of the Campanian (including Bramerton) there seems to be no trend in the development of the cardinalia towards any particular type. I agree here with Popiel-Barczyk (1968 : 23, 24) that the use of minute differences in the cardinalia for distinguishing between species is highly questionable when other features are not taken into account.

External morphology

Sahni (1925, 1929) stressed the importance of the external morphology in distinguishing between the different genera and species of carneithyridines. However, it is notoriously difficult to describe in words a terebratulid in which the two valves are equally biconvex and which has a rectimarginate frontal commissure, strongly incurved beak, indistinct to missing beak ridges, pinhole foramen and no ornament. It is even more difficult to word a differential diagnosis for such forms. As is seen in Sahni (1929 : 57), such short descriptions of the different species must have almost identical wording. It is clear that a statistical approach must be adopted.

In most cases Sahni (1925, 1929) only stated the dimensions of the holotypes and of these only the length of the brachial valve was given in mm while the width, thickness and total length were given as percentages. Most of these types have since been dissected and broken. For statistical purposes I have therefore had to recalculate their dimensions in mm from Sahni's percentages. But in some cases, where the specimen has survived undamaged, I have been able to check the measurements (e.g. the lectotypes of *C. carnea* and *C. elongata*, and the holotype of *C. ornata*). Some of the recalculated dimensions differ from corresponding direct measurements by as much as 5 mm.

The following statistical analyses are based on the length of brachial and pedicle valves, width and thickness. In addition, the diameter of the pedicle foramen and the curvature of the beak have been measured. These measurements are not used in the analyses since it is quite clear that there is no correlation between the curvature of the beak and the outline of the shell, though this was often stressed by Sahni in the diagnosis of a species. The diameter of the foramen is very variable, from

TABLE 2

Monovariate analyses of specimens of Carneithyridinae from different localities

Bramerton

	$\overline{X}$	SD	CV	OR	N
Lp in mm	20·2	2·50	12·38	16·5–23·4	8
Lb in mm	18·4	2·12	11·52	15·2–21·0	8
W in mm	17·3	2·18	12·6	14·4–20·4	8
T in mm	10·8	2·45	22·7	7·5–13·9	7

Wroxham Pipeline

	$\overline{X}$	SD	CV	OR	N
Lp in mm	17·6	2·04	11·6	15·3–19·1	3
Lb in mm	16·0	1·55	25·8	14·3–17·3	3
W in mm	15·4	1·27	8·3	14·4–16·8	3
T in mm	8·9	1·76	19·8	6·9–10·0	3

Thorpe Limekiln

	$\overline{X}$	SD	CV	OR	N
Lp in mm	25·6	4·60	18·0	17·6–33·0	15
Lb in mm	23·4	4·32	18·5	16·0–30·5	15
W in mm	22·2	3·92	17·7	15·8–30·1	15
T in mm	13·4	3·18	23·7	8·5–18·6	15

Whitlingham (Crown Point)

	$\overline{X}$	SD	CV	OR	N
Lp in mm	25·6	4·68	18·3	18·0–34·2	16
Lb in mm	23·4	4·30	18·4	16·3–31·5	16
W in mm	22·3	3·99	17·9	15·6–31·3	16
T in mm	14·1	3·25	23·1	8·4–19·4	16

'Trowse'

	$\overline{X}$	SD	CV	OR	N
Lp in mm	23·6	6·68	28·3	16·2–29·2	3
Lb in mm	21·3	6·09	28·6	14·6–26·5	3
W in mm	21·0	6·90	32·9	14·6–28·3	3
T in mm	13·2	4·69	35·5	8·0–17·1	3

'Thorpe'

	$\overline{X}$	SD	CV	OR	N
Lp in mm	31·5	5·86	18·6	22·6–38·0	6
Lb in mm	28·4	4·82	17·0	20·6–34·0	6
W in mm	27·6	5·45	19·7	21·0–36·0	6
T in mm	17·6	4·42	25·1	11·8–23·8	6

Frettenham

	$\overline{X}$	SD	CV	OR	N
Lp in mm	31·1	6·57	21·1	23·8–37·8	7
Lb in mm	28·3	4·72	16·7	21·7–34·3	7
W in mm	26·9	3·37	12·5	22·0–31·6	7
T in mm	17·4	3·72	21·4	13·4–21·8	7

TABLE 2 (Continued)

Westlegate

	X̄	SD	CV	OR	N
Lp in mm	27·5	5·05	18·4	21·0–35·0	7
Lb in mm	25·2	4·62	18·3	19·2–32·0	7
W in mm	24·6	4·79	19·5	18·8–30·4	7
T in mm	15·3	3·28	21·4	11·4–20·5	7

Caistor St Edmunds

	X̄	SD	CV	OR	N
Lp in mm	22·5	4·45	19·8	14·5–31·0	13
Lb in mm	20·6	4·22	20·5	13·0–28·5	13
W in mm	20·8	3·83	18·4	14·0–29·0	13
T in mm	11·7	2·96	25·3	6·3–17·0	13

Mousehold

	X̄	SD	CV	OR	N
Lp in mm	31·7	3·95	12·5	21·6–39·5	74
Lb in mm	28·7	3·55	12·4	20·0–36·0	74
W in mm	27·1	3·23	11·9	18·5–32·4	74
T in mm	18·1	3·01	16·6	10·6–26·0	74

Catton Grove + 'Catton'

	X̄	SD	CV	OR	N
Lp in mm	28·3	5·87	20·7	13·8–43·9	31
Lb in mm	25·8	5·40	20·9	13·0–40·2	31
W in mm	23·9	4·65	19·5	12·5–36·0	31
T in mm	16·0	4·16	26·0	6·3–26·0	31

Harford Bridges

	X̄	SD	CV	OR	N
Lp in mm	28·5	5·37	18·8	18·8–38·4	23
Lb in mm	26·0	4·94	19·0	16·8–35·5	23
W in mm	23·8	4·89	20·6	16·4–33·5	23
T in mm	16·8	3·76	22·4	10·0–22·0	23

Abbreviations. Lp: length of pedicle valve. Lb: length of brachial valve. W: width. T: thickness. N: number of specimens. X̄: computed mean value. SD: standard deviation. CV: coefficient of variation. OR: observed range.

0·1 mm to 2·0 mm, and cannot be connected with any particular shape of shell. However, there may be a connection with the thickness of the valves since mature specimens with large foramina tend to have thin valves.

Statistical analyses

The *t*-test was applied to the mean values of the lengths of the brachial valves for pairs of the localities represented in Table 2 after the *F*-test had shown that the variances can be considered equal (Simpson *et al.* 1960). The results are given in Table 3. They support the evidence of a decrease in size of mature specimens towards the top of the Campanian given by the histograms in Fig. 3. The only locality which shows an aberrant size distribution is Caistor St Edmunds which is of approximately the same stratigraphical age as Westlegate and Mousehold.

TABLE 3

Monovariate analyses : the *t*-test applied to the mean values of the lengths of the brachial valves, for pairs of the localities represented in Table 2

	t	df	< *P* <	
Bramerton versus Thorpe Limekiln	3·0718	21	0·1%	1%
Bramerton versus Mousehold	8·1580	80		0·1%
Bramerton versus Harford Bridges	*4·1889	29		0·1%
Thorpe Limekiln versus Whitlingham	0·003	29	90%	
Thorpe Limekiln versus 'Trowse'	0·7186	16	40%	50%
Thorpe Limekiln versus 'Thorpe'	2·3091	19	2%	5%
Whitlingham versus Mousehold	5·2807	88		0·1%
'Trowse' versus 'Thorpe'	1·9113	7	5%	10%
'Trowse' versus Mousehold	3·4916	75		0·1%
'Thorpe' versus Mousehold	0·2186	78	80%	90%
Frettenham versus Whitlingham	2·6160	24	1%	2%
Frettenham versus Westlegate	1·2590	12	20%	30%
Frettenham versus Caistor St Edmunds	4·5096	18		0·1%
Frettenham versus Mousehold	0·2491	79	80%	90%
Westlegate versus Caistor St Edmunds	2·2470	18	2%	5%
Caistor St Edmunds versus Whitlingham	1·7421	26	5%	10%
Caistor St Edmunds versus Mousehold	7·4508	85		0·1%
Mousehold versus Catton Grove + 'Catton'	*3·2905	103	0·1%	1%
Mousehold versus Harford Bridges	*2·8615	95	0·1%	1%
Catton Grove + 'Catton' versus Harford Bridges	0·1797	52	80%	90%

* In these cases the *F*-test gave a $P < 5\%$; nevertheless the *t*-test was made.
df: degrees of freedom.
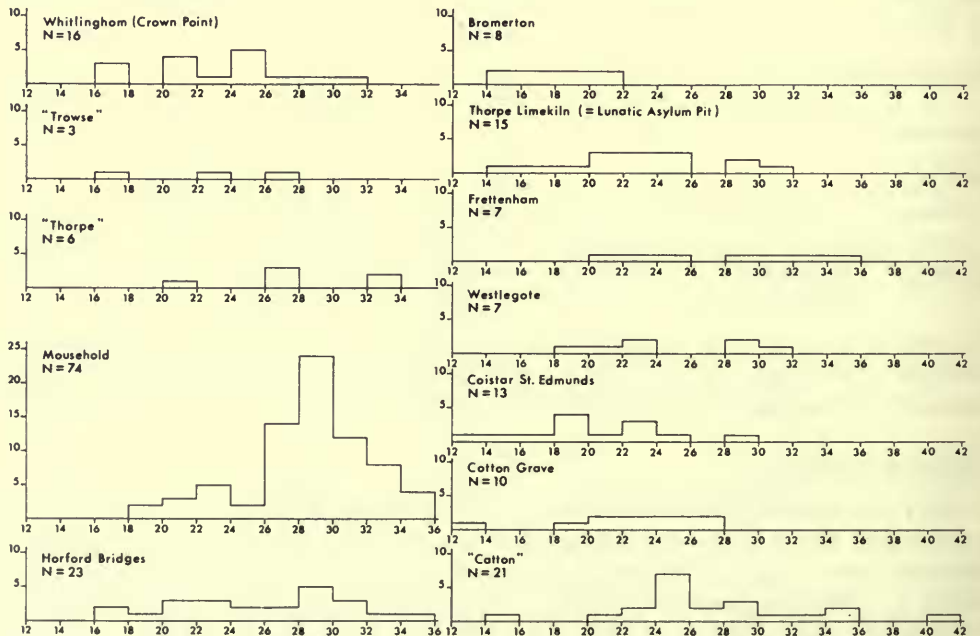
FIG. 3.   Size-frequency histograms of the measurable specimens from 12 localities. Abscissa : length of brachial valve in mm ; ordinate : number of specimens.

Figs 4–12 are length of brachial valve/width and thickness/width scatter diagrams from the 12 localities used in the monovariate analyses. Regression lines (least square method) are drawn for each graph and the equations for the lines are given in Table 4. For the calculation of the regression lines the original measurements have been used, since the scatter diagrams show a linear trend with an elliptical distribution of the plots, and not a fan-shape which would have necessitated use of logarithms (Christensen 1973, 1974).

TABLE 4

Equations for the regression lines of each graph shown in Figs 4–12

		Y = a + bX	sd	r	N
Bramerton	Lb =	2·1036 + 0·9405W	0·8441	0·9295	8
	T =	−7·1429 + 1·0483W	0·8095	0·9533	7
Thorpe Limekiln	Lb =	0·2834 + 1·0407W	1·4610	0·9453	15
	T =	−5·6774 + 0·6926W	1·7081	0·7712	15
Whitlingham (Crown Point)	Lb =	1·0461 + 1·0027W	1·6241	0·9309	16
	T =	−0·4535 + 0·6527W	2·0052	0·8022	16
Frettenham	Lb =	−8·2010 + 1·3587W	1·2821	0·9688	7
	T =	−9·9033 + 1·0150W	1·5976	0·9198	7
Westlegate	Lb =	2·5293 + 0·9226W	1·4662	0·9572	7
	T =	1·5918 + 0·5588W	2·0793	0·8156	7
'Trowse' + 'Thorpe'	Lb =	3·4019 + 0·8893W	1·9497	0·9530	9
	T =	−2·0128 + 0·7141W	1·2374	0·9699	9
Caistor St Edmunds	Lb =	−1·6418 + 1·0713W	1·0104	0·9733	13
	T =	−3·6525 + 0·7391W	0·9155	0·9565	13
Mousehold	Lb =	1·7163 + 0·9965W	1·3918	0·9187	74
	T =	−1·9247 + 0·7399W	1·8529	0·7918	74
Catton Grove + 'Catton'	Lb =	−1·2261 + 1·1296W	1·2518	0·9737	31
	T =	−3·2015 + 0·8019W	1·8629	0·8977	31
Harford Bridges	Lb =	2·9904 + 0·9663W	1·5428	0·9530	23
	T =	−0·1951 + 0·7124W	1·3599	0·9348	23

sd: standard deviation of the regression line. r: coefficient of correlation. Other abbreviations as in Table 2.

Though the regression lines were calculated on the bases of plots of mature and gerontic specimens they can to some extent be compared with the growth curves for the brachiopods. In order to test this, regression lines were calculated for most of the localities on the basis of growth line measurements on the specimens. The resulting regression lines were parallel to the straight middle part of the S-shaped growth curve for the specimens (not figured here). The regression lines based on growth line measurements were roughly parallel to the regression lines based on plots of mature and gerontic specimens, though the first mentioned sloped slightly
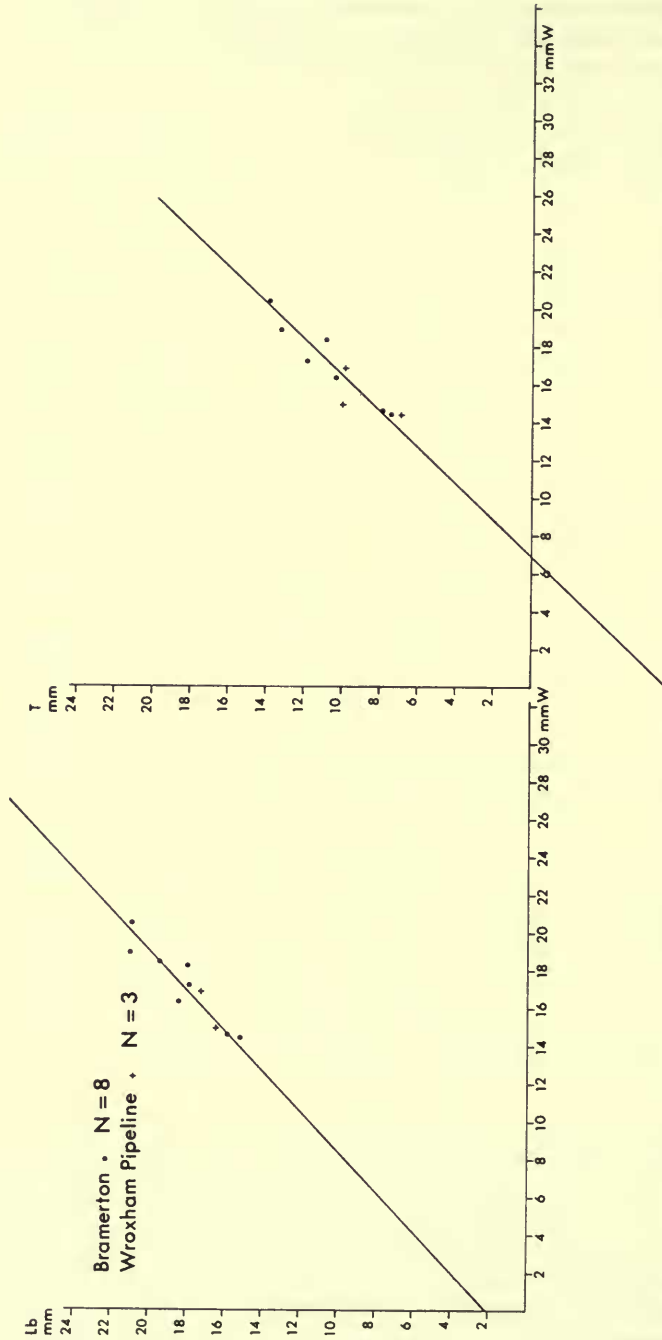
FIG. 4. Length of brachial valve/width and thickness/width scatter diagrams for Bramerton and Wroxham Pipeline localities. Equations for the regression lines, which are based on the Bramerton material only, are given in Table 4.
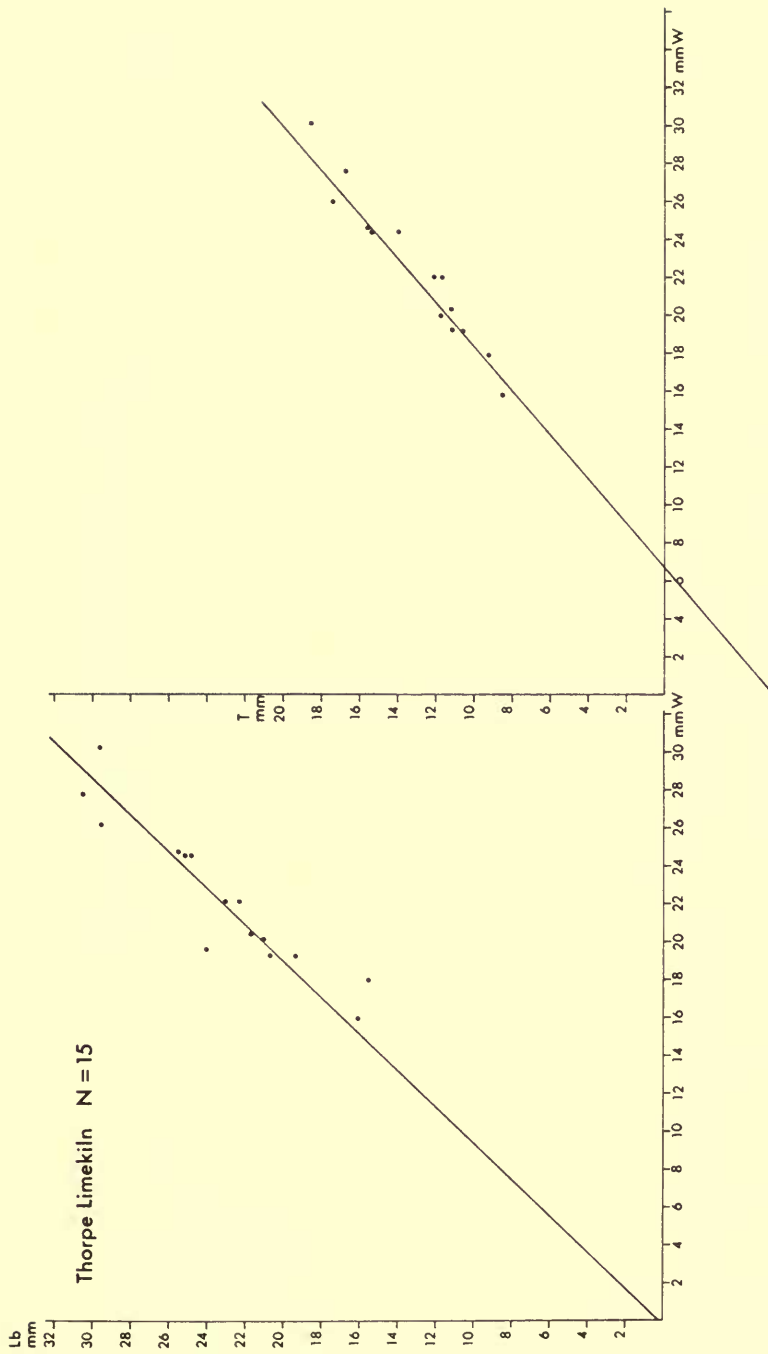
Fig. 5. Length of brachial valve/width and thickness/width scatter diagrams for Thorpe Limekiln locality. Equations for the regression lines are given in Table 4.
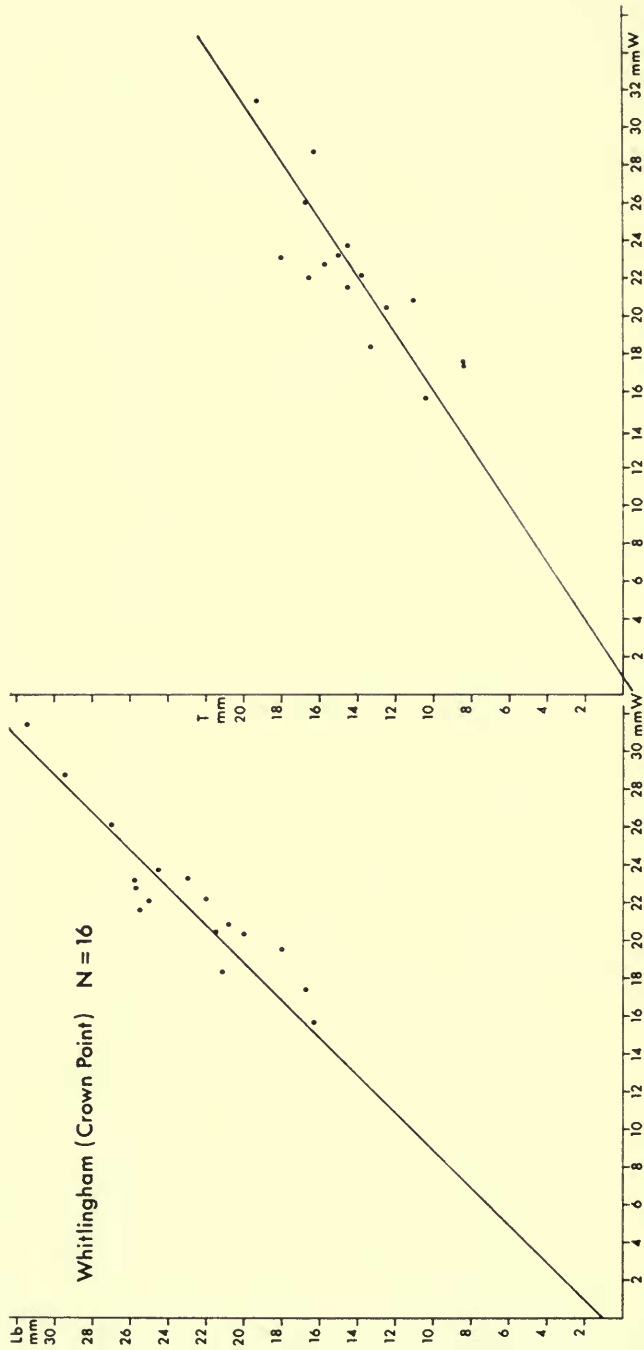
Fig. 6. Length of brachial valve/width and thickness/width scatter diagrams for Whitlingham (Crown Point) Pit locality. Equations for the regression lines are given in Table 4.

Fig. 7. Length of brachial valve/width and thickness/width composite scatter diagrams for specimens from 'Trowse' and 'Thorpe', including the lectotypes of *Carneithyris carnea* and *C. elongata* and the holotypes of *C. uniplicata, C. ornata* and *Magnithyris magna*. Though there is a difference in geological age between the localities covered by the names 'Trowse' and 'Thorpe', they have been combined as one in the bivariate statistical analyses. Equations for the regression lines are given in Table 4.

FIG. 8.   Length of brachial valve/width and thickness/width scatter diagrams for the Caistor St Edmunds, Frettenham, and Westlegate localities.

more steeply and had a lower intercept on the ordinate. The two sets of regression lines were tested by the t-test and in all cases the differences in slopes were found to be insignificant ($P > 80\%$), and thus the regression lines in Figs 4–12 can roughly be considered to represent the straight middle part of the growth curves for the specimens from the different localities.

The t-test was applied to the slopes of the regression lines for pairs of localities after the F-test had shown that the variances can be considered equal. The results are given in Table 5. The differences in slope can nowhere be considered highly significant.

TABLE 5

Bivariate analyses. Test for differences in the slopes of regression lines for the pairs of localities shown in Table 3.

		t	df	$< P <$	
Bramerton versus Thorpe Limekiln	Lb/W	0·4000	19	70%	80%
	T/W	1·2017	18	20%	30%
Bramerton versus Whitlingham (Crown Point)	Lb/W	0·2260	20	80%	90%
	*T/W	1·1489	19	20%	30%
Bramerton versus 'Trowse' + 'Thorpe'	*Lb/W	0·1692	13	80%	90%
	T/W	1·6169	12	10%	20%
Bramerton versus Frettenham	Lb/W	1·5974	11	10%	20%
	T/W	0·1196	10	90%	
Bramerton versus Westlegate	Lb/W	0·0767	11	90%	
	*T/W	1·5342	10	10%	20%
Bramerton versus Caistor St Edmunds	Lb/W	0·7001	17	40%	50%
	T/W	1·7647	16	5%	10%
Bramerton versus Mousehold	Lb/W	0·0224	78	90%	
	*T/W	0·9147	77	30%	40%
Bramerton versus Catton Grove + 'Catton'	Lb/W	1·6147	35	10%	20%
	*T/W	0·7515	34	40%	50%
Bramerton versus Harford Bridges	Lb/W	0·0980	27	90%	
	T/W	1·4005	26	80%	90%
Thorpe Limekiln versus Whitlingham (Crown Point)	Lb/W	0·2612	27	70%	80%
	T/W	0·2272	27	80%	90%
Thorpe Limekiln versus Mousehold	Lb/W	0·4081	85	60%	70%
	T/W	0·3345	85	70%	80%
Whitlingham (Crown Point) versus Mousehold	Lb/W	0·0583	86	90%	
	T/W	0·6254	86	50%	60%
'Trowse' + 'Thorpe' versus Mousehold	Lb/W	1·1247	79	20%	30%
	T/W	0·2172	79	80%	90%
'Trowse' + 'Thorpe' versus Harford Bridges	Lb/W	0·6657	28	50%	60%
	T/W	0·0183	28	90%	

TABLE 5 (Continued)

		t	df	$< P <$	
Frettenham versus Westlegate	Lb/W	2·1371	10	5%	10%
	T/W	1·6606	10	20%	30%
Frettenham versus Caistor St Edmunds	Lb/W	1·8265	16	10%	20%
	T/W	1·6494	16	10%	20%
Frettenham versus Mousehold	Lb/W	2·0673	77	2%	5%
	T/W	1·1835	77	20%	30%
Frettenham versus Harford Bridges	Lb/W	2·0645	26	2%	5%
	T/W	1·6614	26	10%	20%
Westlegate versus Caistor St Edmunds	Lb/W	1·1150	16	20%	30%
	*T/W	1·1414	16	20%	30%
Westlegate versus Mousehold	Lb/W	0·5711	77	50%	60%
	T/W	1·0462	77	20%	30%
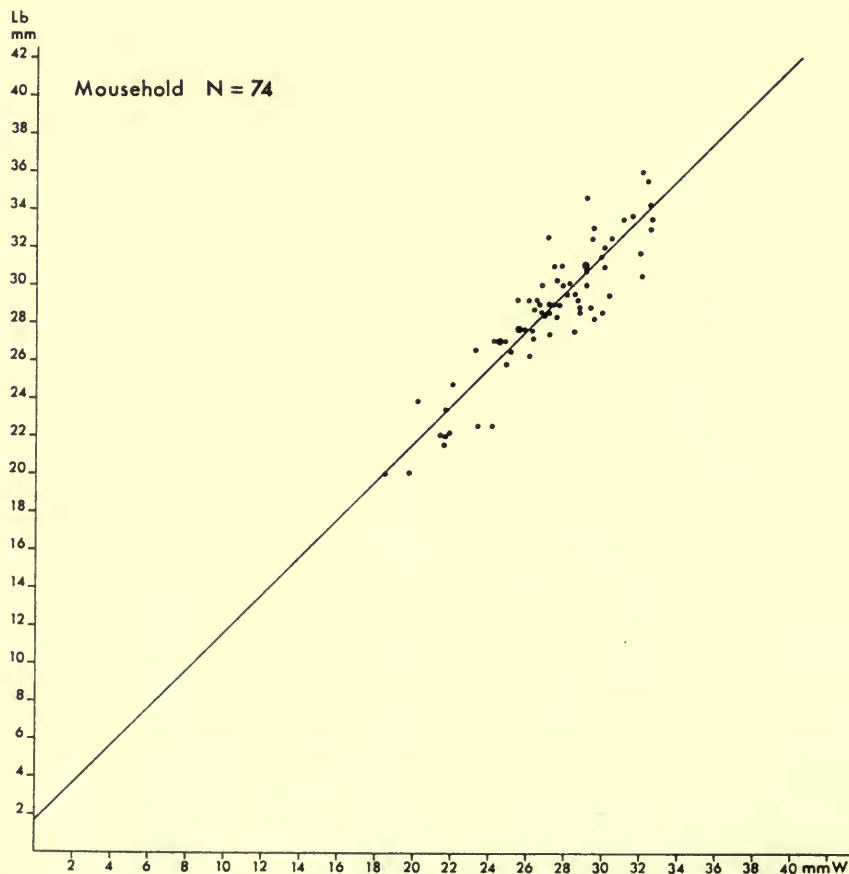
Fig. 9. Length of brachial valve/width scatter diagram for Mousehold locality.

TABLE 5 (Continued)

		t	df	$< P <$	
Caistor St Edmunds versus Mousehold	Lb/W	0·6636	83	50%	60%
	*T/W	0·0054	83	90%	
Mousehold versus Catton Grove + 'Catton'	Lb/W	1·8403	101	5%	10%
	T/W	0·6250	101	50%	60%
Mousehold versus Harford Bridges	Lb/W	0·3738	93	70%	80%
	T/W	0·2770	93	70%	80%
Catton Grove + 'Catton' versus	Lb/W	2·0193	50	5%	10%
Harford Bridges	T/W	0·9154	50	30%	40%

* In these cases the F-test gave a $P < 5\%$; nevertheless the t-test was made.
Abbreviations as in Tables 2 and 3.

In Figs 13 and 14 the regression lines for the different localities have been super-imposed to give a visual impression of similarities of growth in the specimens ; the only aberrant localities are Frettenham and Bramerton. The material from Frettenham shows a slightly more rapid growth in length of brachial valve than that of the other localities, while both Bramerton and Frettenham show a steeper increase in thickness with width than the other localities.

Twenty-seven specimens were plotted for length of brachial valve against width ; these including the holotypes of *Carneithyris subpentagonalis, C. circularis, C.*
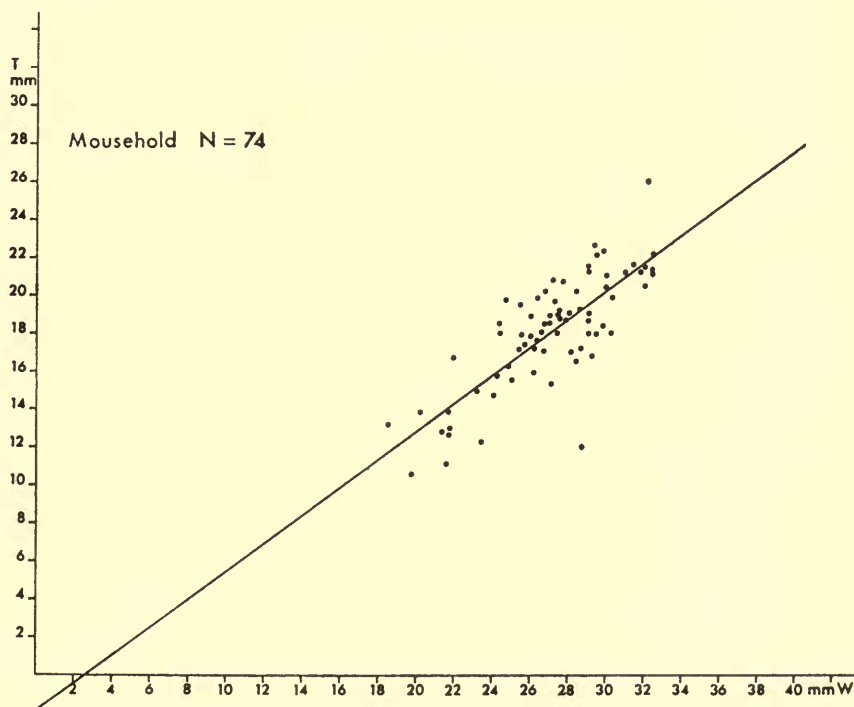
FIG. 10.   Thickness/width scatter diagram for Mousehold locality.
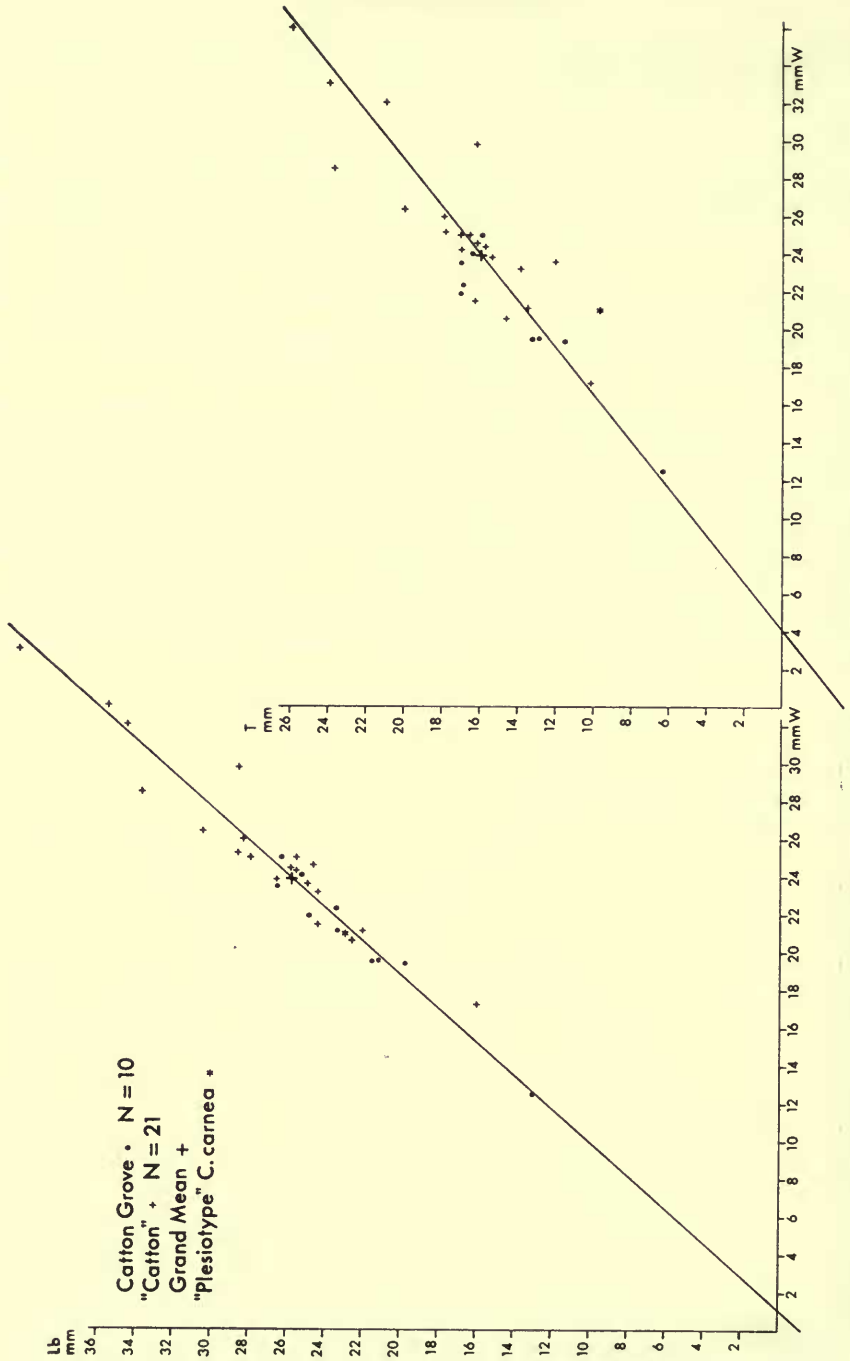
FIG. 11. Length of brachial valve/width and thickness/width scatter diagrams for Catton Grove + 'Catton' localities.
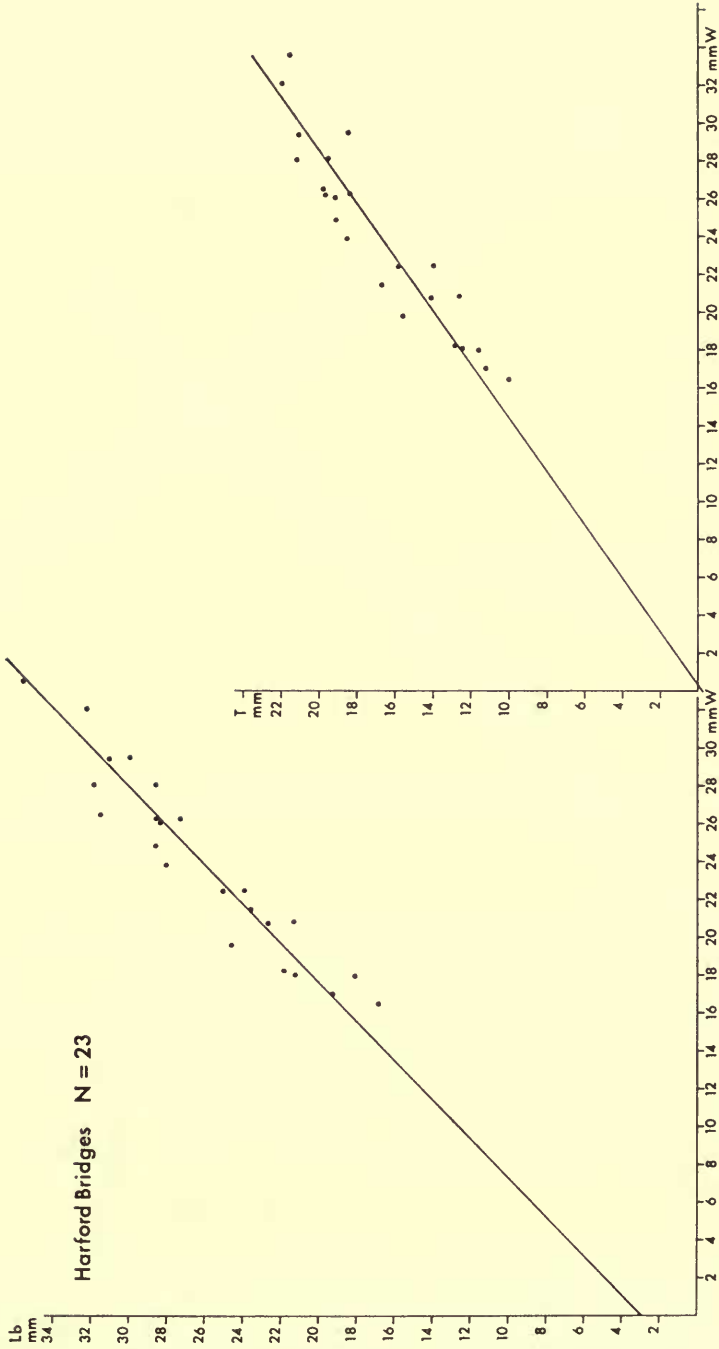
FIG. 12. Length of brachial valve/width and thickness/width scatter diagrams for Harford Bridges locality.

variabilis, *C. acuminata*, *C. norvicensis*, *C. subovalis*, *C. daviesi*, *Pulchrithyris extensa*, *Ellipsothyris similis*, *Chatwinothyris symphytica*, *Ornithothyris carinata*, *Magnithyris truncata* and paratypes of *Carneithyris subpentagonalis*, *C. circularis*, *C. variabilis*, *C. daviesi*, *Ellipsothyris similis* and *Magnithyris magna*. They are all from old collections with no locality specification and all were identified by Sahni. The regression line was computed (least square method) and gave the following result : Lb = 22·6890 + 0·3311W ; sd = 3·8349 ; r = 0·4348. This regression line is
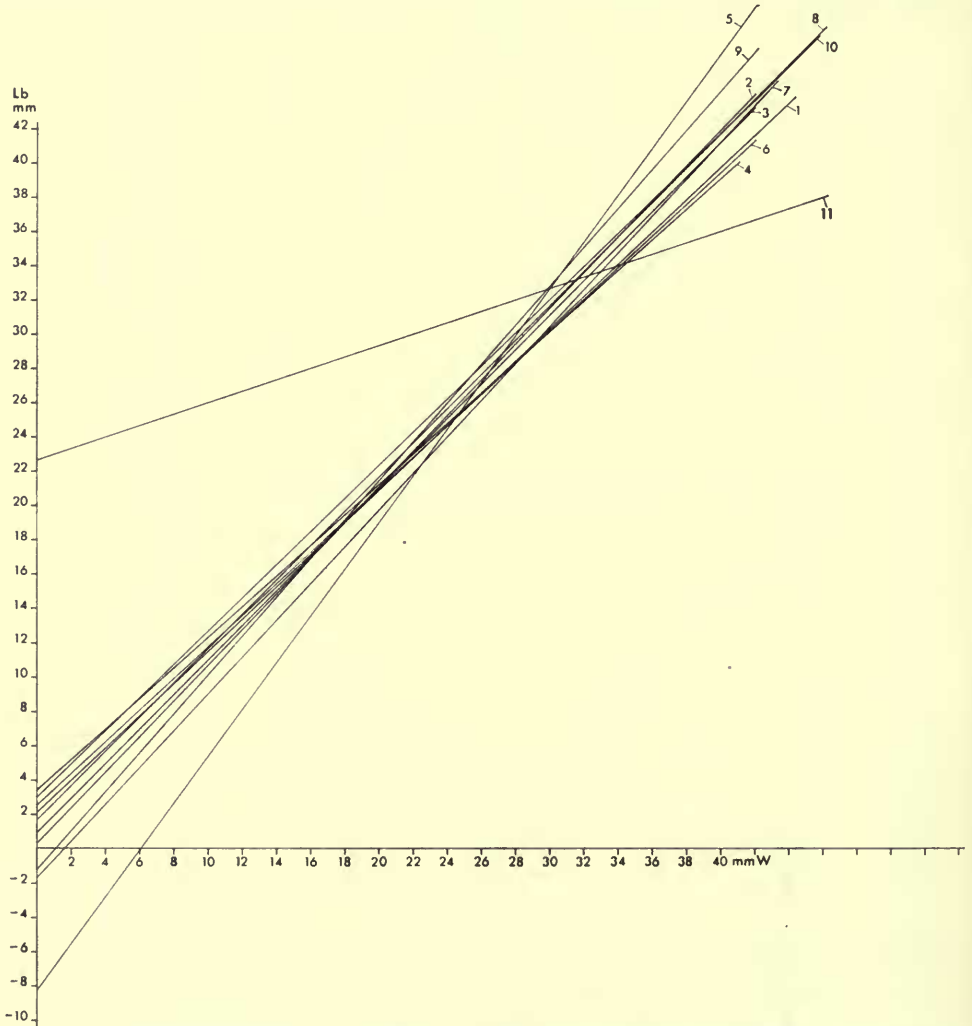
FIG. 13. Length of brachial valve/width. Superimposed regression lines for the material from the 10 localities used in the bivariate analyses. 1 : Bramerton ; 2 : Thorpe Limekiln ; 3 : Whitlingham (Crown Point) ; 4 : 'Trowse' + 'Thorpe' ; 5 : Frettenham (note the steep slope) ; 6 : Westlegate ; 7 : Caistor St Edmunds ; 8 : Mousehold ; 9 : Catton Grove + 'Catton' ; 10 : Harford Bridges. 11 : regression line based on the 27 gerontic specimens discussed on p. 359.
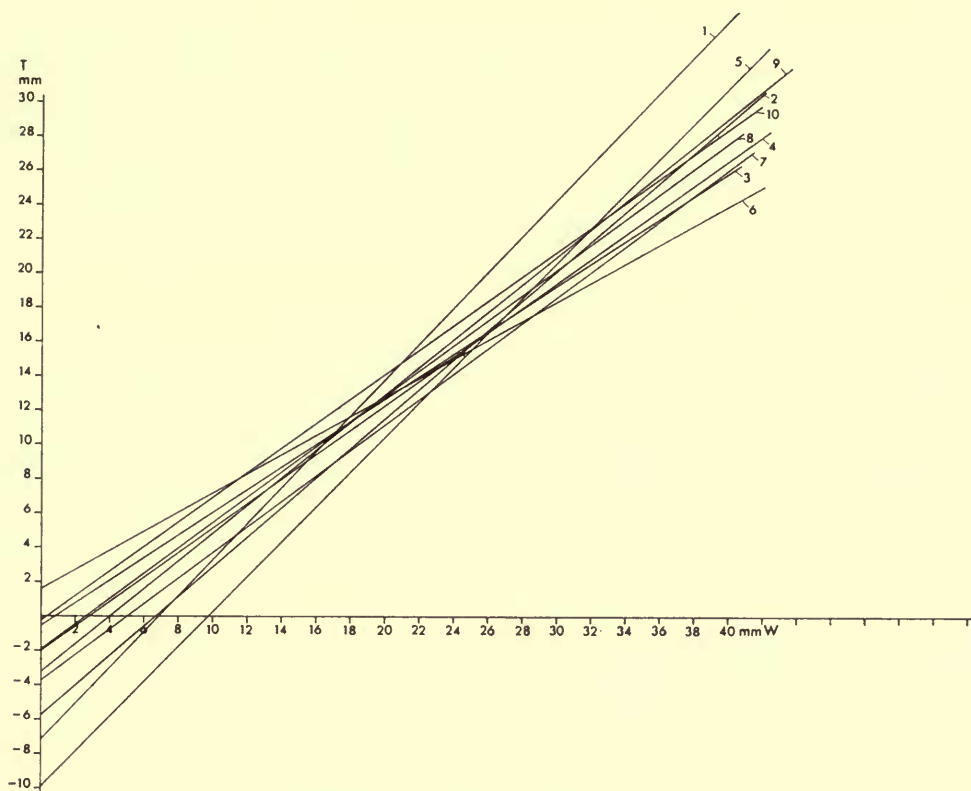
FIG. 14.   Thickness/width.   Superimposed regression lines for the same localities as in
   Fig. 13.   Note the steep slopes for Bramerton and Frettenham ; the two lines are
   approximately parallel.

included in Fig. 13 (no. 11) but shows a striking difference from the others.   The
slope of the line reflects the upper part of the S-shaped growth curve of the brachio-
pods in general, demonstrating the slow growth of senile specimens.   It was partly
on the basis of the differences in outline that Sahni established his many genera and
species ; the great variation in outline of these 27 senile specimens is well documented
by the low correlation coefficient.

In contrast to the 27 senile specimens, however, the types from known localities
fit well into the linear scatter plots, and the plots show high correlation, e.g. 'Trowse'
and 'Thorpe' (Fig. 7).

Conclusions

It can be concluded from the statistical analyses here offered that the present
material from known localities shows no significant differences in growth and outline
that can be used for differentiating species.   The 27 unlocated senile specimens on
which 12 species were erected by Sahni demonstrate the wide variation in shape

naturally to be found in gerontic material of any species, while localized type-specimens all fit into the scatter plot for their locality. It is also concluded that differences in the cardinalia demonstrated in the often gerontic types cannot be used to distinguish between species of *Carneithyris* in the English Campanian. Neither the growth of the specimens, their outline nor their cardinalia show any distinct trend which may be used for erecting species on a stratigraphical or geographical basis. In the available material I can recognize only one species of *Carneithyris* in the Upper Campanian of England, namely *C. carnea* (J. Sowerby).

VII. CONCLUDING REMARKS

On the basis of the present material I am unable to subdivide the Campanian carneithyridines into species which are visibly distinguishable or statistically valid. In the specimens from the Upper Campanian the only trend which I have detected is a tendency to develop smaller mature individuals towards the Campanian–Maastrichtian boundary. Single specimens, including those called *Magnithyris* and *Carneithyris circularis* by Sahni, seem to have retained to a great age certain juvenile characters such as thin shells, a circular outline, a beak which is not strongly incurved and a fairly large foramen. However, these and other external and internal features do not appear in any particular facies or horizon. On the contrary, they show a scattered occurrence throughout the Upper Campanian of Norfolk and can be considered to be due to peculiarities in the genetical composition of the individuals concerned. I thus consider that all the available carneithyridines from the Upper Campanian of Norfolk should be referred to the single species *Carneithyris carnea*.

In the Lower Maastrichtian chalk of Sidestrand and Trimingham, *C. carnea* is replaced by *C. subcardinalis* (Sahni), which is distinguishable from *C. carnea* on the basis of its internal features. Unfortunately the critical sediments at the Campanian–Maastrichtian boundary are not exposed in Norfolk and the replacement of the one species by the other, which would establish whether it is gradual, sharp or with overlap, cannot be studied in detail. *C. carnea* is still present at Bramerton and *C. subcardinalis* is found in the lowest exposed Maastrichtian at Sidestrand.

The subfamily Carneithyridinae thus contains only one genus, *Carneithyris*, the stratigraphical range of which is poorly known. Muir-Wood (1965) offered no suggestions as to the phyletic relationships of the subfamily ; its sudden appearance in the Upper Campanian of north-west Europe is, so far, an enigma. Some terebratulids from the Lower Campanian of the Hampshire Basin (R. M. Brydone collection, Institute of Geological Sciences, London) resemble carneithyridines externally but they have not been opened and dissected. Apart from these uncertain specimens, no carneithyridines are known of pre-Upper Campanian age. *Carneithyris* is known from the Maastrichtian and Danian of northern Europe (Asgaard 1963, 1970 ; Steinich 1965 ; Popiel-Barczyk 1968 ; Surlyk 1972).

Carneithyris probably invaded the chalk facies from a more coastal area, its ancestors having been 'normal' terebratulids with clearly distinguished cardinalia with ventrally concave outer hinge-plates (as seen in the specimen called *Magnithyris truncata*) and a stout functional pedicle. An experimental phase was passed through

in the Upper Campanian chalk where the animals retained a thin, functional pedicle, possibly fastened to a small object as substrate used as a drag anchor, as seen in the Recent terebratellid *Laqueus californianus* on coarse sandy bottoms. During this phase a heavy posterior end with swollen and fused cardinalia was developed. In the Maastrichtian, *Carneithyris* increased the weight of the callus deposits in the posterior part of the valves and blocked the foramen, thereby becoming perfectly adapted for a free-living life habit as a 'self-righting tumbler' in the soft, fine-grained sea floor (Steinich 1965 ; Surlyk 1972). Stocks in the marginal calcarenite facies meanwhile retained a functional pedicle and had a less heavily weighted shell.

In Denmark and Sweden, *Carneithyris* disappeared with the introduction of calcarenite facies in the lowermost Tertiary and first migrated back into this area in the Middle Danian. In the calcarenite facies the genus developed a sulcate frontal commissure which was possibly a further development of the slightly sulcate to paraplicate commissure seen in some specimens from high Paramoudra Chalk and Bramerton, Norfolk. The Danian specimens furthermore have cardinalia very much like those of the Campanian *C. carnea* and in most cases they possessed a functional, though very slender pedicle (Asgaard 1963).

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PLATE 1

PLATE 2

Carneithyris elongata (J. de C. Sowerby, 1823) (p. 327, see also Pl. 4, fig. 5)

FIG. 1a–c.   Lectotype, B 49823, × 2.
FIG. 2a, b.   Paralectotype, B 49824, dorsal and anterior-dorsal views, × 2.
FIG. 3a–c.   Davidson's specimen, B 6101, × 2.

Chatwinothyris symphytica Sahni, 1925 (p. 336)

FIG. 4.   Holotype, GSM 47523, detail of cardinalia, × 4.   Note the pitted callus deposits and the extremely prominent cardinal process.

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PLATE 2

PLATE 3

Carneithyris circularis Sahni, 1925 (p. 328, see also Pl. 4, figs 6, 7)

FIG. 1a–c.   Paratype, B 49862, × 2.
FIG. 2a, b.   Paratype, B 45603, × 2 ; detail of cardinalia, × 4.

Carneithyris carnea (J. Sowerby, 1812) (p. 326, see also Pl. 1, figs 1–3)

FIG. 3a, b.   'Plesiotype', B 45600, × 2 ; detail of cardinalia, × 4.

Piarothyris rotunda Sahni, 1925 (p. 334)

FIG. 4.   Holotype, 18 KCN, detail of cardinalia, × 4.
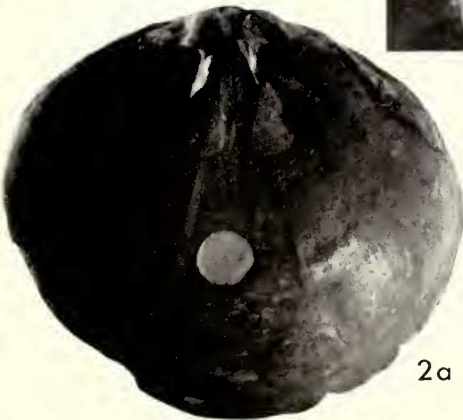
PLATE 3

PLATE 4

All figures except Fig. 11 show details of the cardinalia.

Magnithyris magna Sahni, 1925 (p. 333, see also Pl. 5, fig. 10)

Fig. 1.   Holotype, GSM 48488, × 4.

Magnithyris truncata Sahni, 1929 (p. 334)

Fig. 2.   Holotype, B 45606, × 4.

Carneithyris subovalis Sahni, 1925a (p. 330)

Fig. 3.   Holotype, B 15159, × 4.
Fig. 4.   Paratype, Norwich Castle Museum, no number, × 4.

Carneithyris elongata (J. de C. Sowerby, 1823) (p. 327, see also Pl. 2, figs 1–3)

Fig. 5.   'Plesiotype', B 45243, × 4.

Carneithyris circularis Sahni, 1925 (p. 328, see also Pl. 3, figs 1, 2)

Fig. 6.   Holotype, 15 KCN, × 4.
Fig. 7.   Paratype, B 45604, × 4.

Pulchrithyris extensa Sahni, 1925 (p. 333)

Fig. 8.   Holotype, 7 KCN.   Ventral view of the remains of the brachial valve, × 4.

Carneithyris uniplicata Sahni, 1925a (p. 330)

Fig. 9.   Holotype, GSM 48518, × 4.

Ellipsothyris similis Sahni, 1925 (p. 334, see also Pl. 7, fig. 5)

Fig. 10.   Holotype, 14 KCN, × 4.

Carneithyris ornata Sahni, 1929 (p. 331)

Fig. 11.   Holotype, GSM 48498.   Dorsal view of brachial valve, × 2.
Fig. 12.   Same, ventral view of the posterior part of the brachial valve, showing cardinalia, very clear muscle impressions, and slightly pitted callus, × 4.

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PLATE 4

PLATE 5

All figures show details of the cardinalia.

Carneithyris variabilis Sahni, 1925 (p. 328, see also Pl. 7, fig. 4)

FIG. 1.   Holotype, 14 CMN, × 4.

Ornithothyris carinata Sahni, 1925 (p. 335)

FIG. 2.   Holotype, 17 KCN, × 4.

Carneithyris acuminata Sahni, 1925 (p. 329)

FIG. 3.   Holotype, 19 CMN, × 4.

Pulchrithyris gracilis Sahni, 1925 (p. 332)

FIG. 4.   B 98123, × 4.
FIG. 5.   B 46300, × 4.
FIG. 6.   Paratype, GSM 48485, × 4 ; the loop is glued on upside down.
FIG. 7.   Holotype, GSM 48487, × 4.

Carneithyris norvicensis Sahni, 1925 (p. 329, see also Pl. 6, fig. 5)

FIG. 8.   Possible paratype, B 52067, × 4.
FIG. 11.   Holotype, GSM 44494, × 4.

Carneithyris cf. *carnea* (J. Sowerby) (p. 326)

FIG. 9.   27 KCN, × 4.

Magnithyris magna Sahni, 1925 (p. 333, see also Pl. 4, fig. 1)

FIG. 10.   Presumed paratype, B 15149, × 4.

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PLATE 5

PLATE 6

All figures except Figs 1 and 2 show details of the cardinalia.

Carneithyris daviesi Sahni, 1925a (p. 331, see also Pl. 7, fig. 1)

Fɪɢ. 1a, b.   Paratype, B 459, × 2.
Fɪɢ. 2a, b.   Same, details of pedicle valve, oblique views to show the strongly swollen tooth bases, × 4.
Fɪɢ. 3.   Holotype, B 45599, × 4.
Fɪɢ. 4.   The third specimen, B 45642, × 4.

Carneithyris norvicensis Sahni, 1925 (p. 329, see also Pl. 5, figs 8, 11)

Fɪɢ. 5.   Possible paratype, B 45610, × 4.
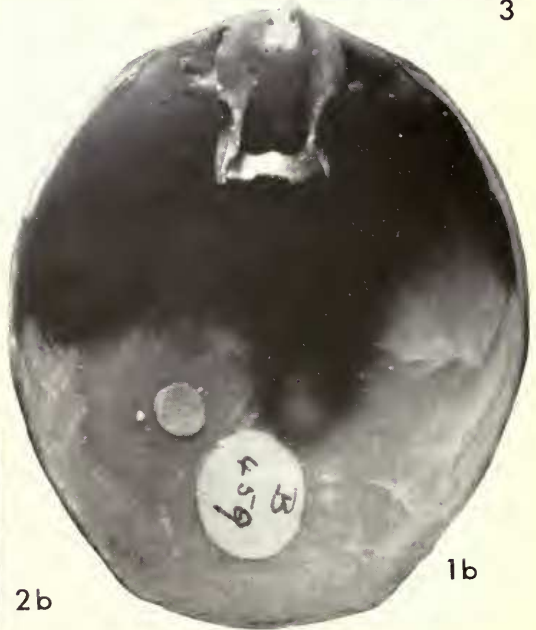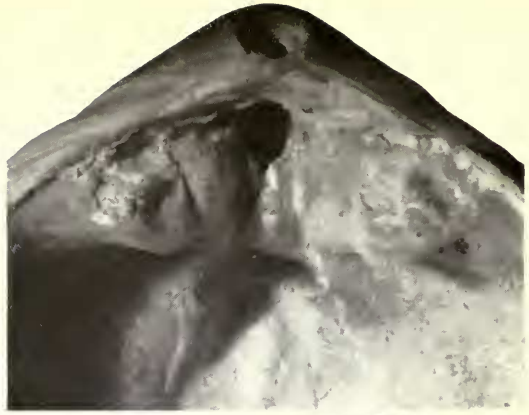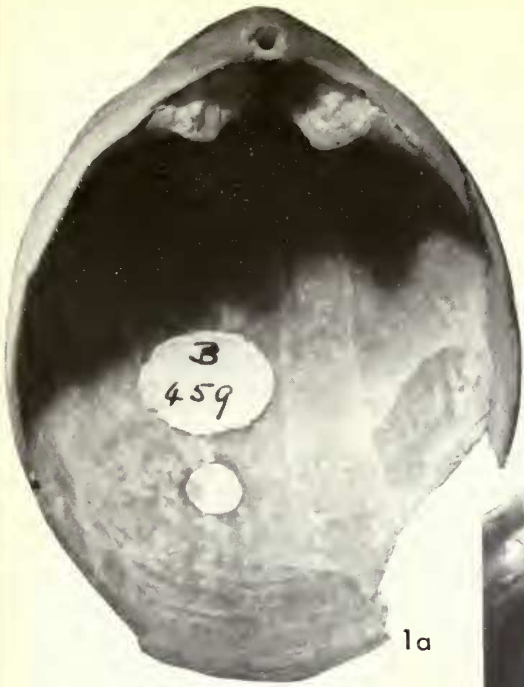
Bull. Br. Mus. nat. Hist. (Geol.) 25, 5

PLATE 6

All figures show details of the cardinalia.

Carneithyris daviesi Sahni, 1925a (p. 331, see also Pl. 6, figs 1–4)

Fig. 1a–c.   Paratype, B 459, ventro-lateral, ventral and ventro-posterior views, × 4.

Carneithyris subpentagonalis Sahni, 1925 (p. 327)

Fig. 2a, b.   Holotype, 8 KCN, ventro-lateral and ventral views, × 4.
Fig. 3.   Paratype, GSM 44491, ventral view, × 4.
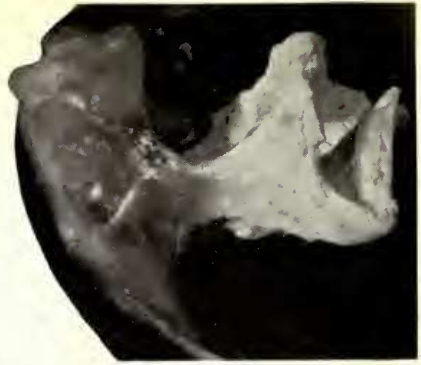
Carneithyris variabilis Sahni, 1925 (p. 328, see also Pl. 5, fig. 1)

Fig. 4.   Paratype, 13 CMN, ventral view, × 4.

Ellipsothyris similis Sahni, 1925 (p. 334, see also Pl. 4, fig. 10)

Fig. 5.   ? Paratype, B 45653, ventral view, × 4.

PLATE 8

All figures show details of the cardinalia.

Chatwinothyris subcardinalis Sahni, 1925 (p. 335)

FIG. 1a–c.   Holotype, GSM 44501, ventral, ventro-posterior and posterior views, × 4.
FIG. 2a, b.   Paratype, B 46326, ventral and ventro-posterior views, × 4.
FIG. 3a, b.   Another specimen, B 46327, ventral and ventro-posterior views, × 4.
FIG. 4a, b.   Another specimen, B 21266, ventral and ventro-posterior views, × 4.

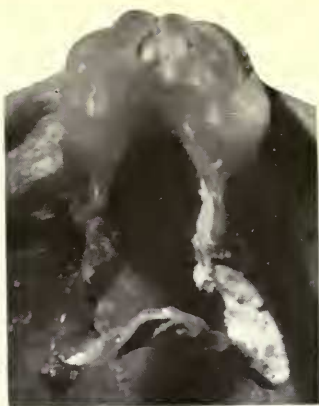### *Chatwinothyris curiosa* Sahni, 1925a (p. 337)

FIG. 5a, b.   Holotype, B 45669, ventral and ventro-posterior views, × 4.
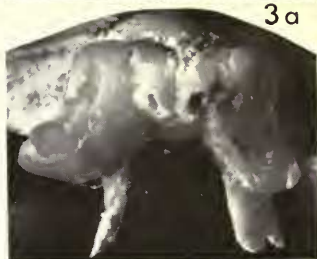FIG. 5c–e.   Same, various oblique views of the cardinalia and brachidium showing the exotic loop, × 4.

PLATE 8